HABITAT VARIATION
AND ITS
INFLUENCE ON THE LOCOMOTOR ECOLOGY
OF
WILD ORANGUTANS

by

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Abstract

Orangutans are the largest arboreal primate and have a diverse locomotor repertoire. The principal aim of this thesis was to explore the dynamic between morphology, behaviour and habitat to better understand the influences on orangutan locomotion. Positional behaviour data was collected at two peat-swamp forest sites: Sabangau, Central Kalimantan; and Suaq Balimbing, Aceh. We quantified forest structure and support availability in the dry-lowland forest of Ketambe, Aceh, in addition to the aforementioned peat-swamp forests and found that the three forests were structurally different. We used a remote measuring technique to compare limb morphology between species, and found they were similar suggesting selection for an optimal limb length. We found that habitat had a stronger influence on locomotion than either species or study site. Orangutans in different habitats had similar profiles of preferred supports, with the exception that the Sumatran species (*Pongo abelii*) had a preference for lianas. Orangutans in Sumatran peat-swamp forest used more compliant supports than recorded in dry-lowland forest. However, pronograde bridging was also used to negotiate the most flexible supports. This thesis has shown that habitat has a strong influence on orangutan locomotor behaviour, which is important since their habitat is becoming increasingly altered through human disturbance.

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CHAPTER 1

General introduction

1.1 Ecomorphology

ECOMORPHOLOGY is the study of the relationship between morphology, ecology and behaviour and how it differs between species (Williams, 1972; Karr and James, 1975). In order to understand how an animal is adapted to function successfully and to understand its physical evolution the interactions between morphology, performance and the structure of the habitat utilised should be assessed (Gomberg et al., 1979; Bock and von Wahlert, 1998). Thus, an important component of ecomorphology are behavioural studies that link traditional functional morphology with ecological investigations (Bock, 1994). Ecomorphological hypotheses generally assume that differences in morphology result in differences in performance capability, which in turn cause differences in ecology or behaviour; and that the evolution of morphology and performance capability are tightly linked (see Garland, 1983; Losos, 1990; Irschik and Garland, 2001). That much can be inferred about a species from

its morphology is often self-evident, for example, flying animals tend to have wings, animals which dig tend to have powerful limbs and claws (Losos, 1990). However, there are also less obvious adaptations which can, nevertheless, dramatically improve performance capability and thus the fitness of a species. Species are adapted to the most demanding behaviours they perform, i.e. behaviours which encounter the most stresses, or sub-maximal stresses regularly, such behaviours may be frequent, or rare, but key to performance success. For example, climbing is demanding particularly for large-bodied animals as it is performed against gravity and is therefore likely to be reflected in the musculoskeletal system, and adaptations to it may outweigh or compete with adaptations to the most frequently performed behaviours that are less demanding. Thus adaptations are a complex compromise between load (i.e. stresses on the musculoskeletal system), frequency and selective benefit e.g. leaping to escape from a predator. Therefore, in order to understand the more subtle adaptations, and thus the evolution of variation, the full repertoire of a species' behaviour must be investigated.

1.2 Orangutan Biology

Taxonomy

Orangutans are classified in the great ape family (Hominoidea), along with gorillas (*Gorilla* spp.), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), and humans (*Homo sapiens*). Traditional classifications of orangutans recognised only one species, with Bornean and Sumatran orangutans being classed as separate sub-species. Today, orangutans are recognised as two separate species, the Sumatran (*Pongo abelii*) and Bornean (*P. pygmaeus*) (Xu

and Arnason, 1996; Zhi et al., 1996; Groves, 2001; Goossens et al., 2009), the Bornean orangutan being classified into three sub-species namely, *P. pygmaeus pygmaeus* from north-west Kalimantan to Sarawak, *P. p. morio* from north-west Kalimantan to Sabah and *P. p. wurmbii* in south-west and central Kalimantan (Xu and Arnason, 1996; Zhi et al., 1996; Groves, 2001; Goossens et al., 2009).

Classifications which recognise two orangutan species are based on morphological, karyological, and genetic studies, which show considerable disparity both between and within Bornean and Sumatran populations (e.g. Bruce and Ayala, 1979; Seuanez et al., 1979; Ferris et al. 1981, Lucotte and Smith, 1982; Dugoujon et al., 1984; Röhrer-Ertl, 1988; Caccone and Powell, 1989; Groves et al., 1992; Ryder and Chemnick, 1993; Ruvolo et al., 1994; Xu and Arnason, 1996; Zhi et al., 1996; Guy et al., 2003).

Distribution

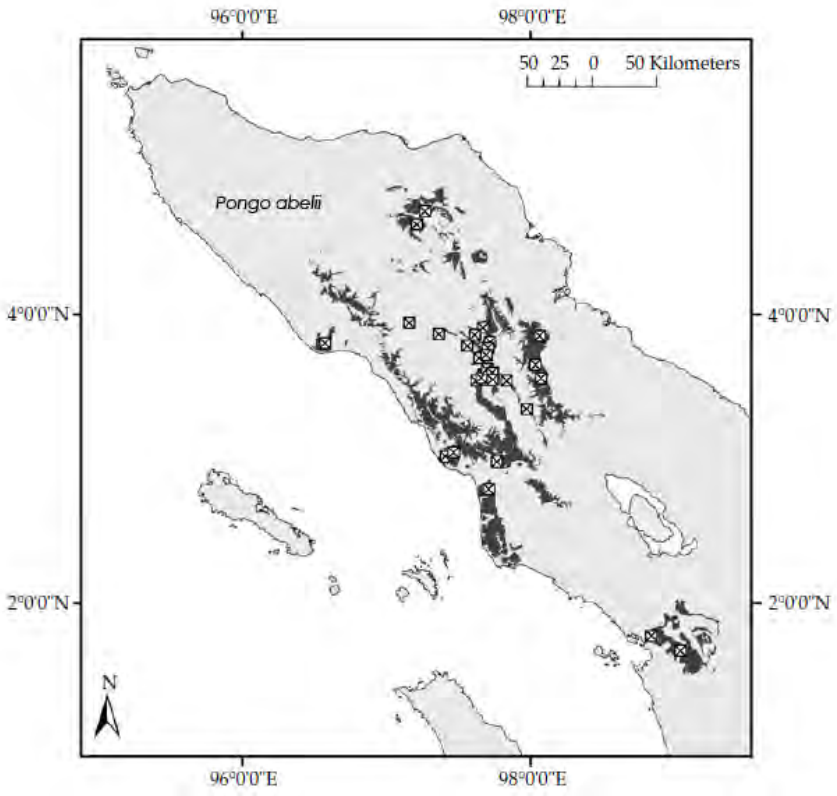
Orangutans are the only living great apes found outside Africa (Delgado and van Schaik, 2000). Molecular studies and fossil data indicate dates of around 13 million years ago (15-12) for orangutan divergence (Fleagle, 1999; Glazko and Nei, 2003). During the Pleistocene epoch, the orangutan ranged throughout both the wet and seasonal tropics, including Java, Sumatra, Borneo, Vietnam, and the subtropical regions of southern China, and from lowland to highland localities, as evidenced by subfossil sites (von Koenigswald, 1982; Rijksen and Meijaard, 1999; Delgado and van Schaik, 2000). Changes in sea levels resulted in repeated exposure of the continental shelf and the formation of land bridges between the islands (Verstappen, 1997; Voris, 2006), allowing species interchange followed by subsequent

isolation (Fordham and Brook, 2010). Orangutans are thought to have entered southern Borneo from Sumatra via the Bangka-Belitung-Karimata land-bridge, which is now submerged (Rijksen and Meijaard, 1999).

Today orangutans only survive on the islands of Borneo and Sumatra, primarily within Indonesia, but also in the Malaysian states of Sabah and Sarawak. The Sumatran population is thought to number around 7,300 individuals (Singleton et al., 2004) and is classified as 'critically endangered' (IUCN, 2012). The population of the Sumatran species is restricted to Northern Sumatra, with the vast majority located within the Leuser Ecosystem in Aceh (Figure 1.1), a province where political unrest and environmental disaster have severely hindered conservation efforts in recent years (Delgado and van Schaik, 2000; Marshall et al., 2009). Population viability analysis (PVA) estimates that habitats capable of supporting more than 250 orangutans are necessary to ensure good demographic and genetic stability (Singleton et al., 2004; Marshall et al., 2009). Of the thirteen identified populations on Sumatra, only six were estimated to have more than 250 individuals, with only three of those thought to support populations in excess of 1,000 individuals (Singleton et al., 2004; Wich et al., 2008).

The population in Borneo numbers around 45,000-69,000 individuals (Singleton et al., 2004; Caldecott and Miles, 2005). The IUCN lists all three Bornean subspecies as 'Endangered' (IUCN, 2012). There was an estimated 306 separate areas of forest of which only 32 are thought to support at least 250 individuals, with a mere 17 containing a population of more than 1,000 individuals (Figure 1.2; Singleton et al., 2004; Wich et al., 2008). The

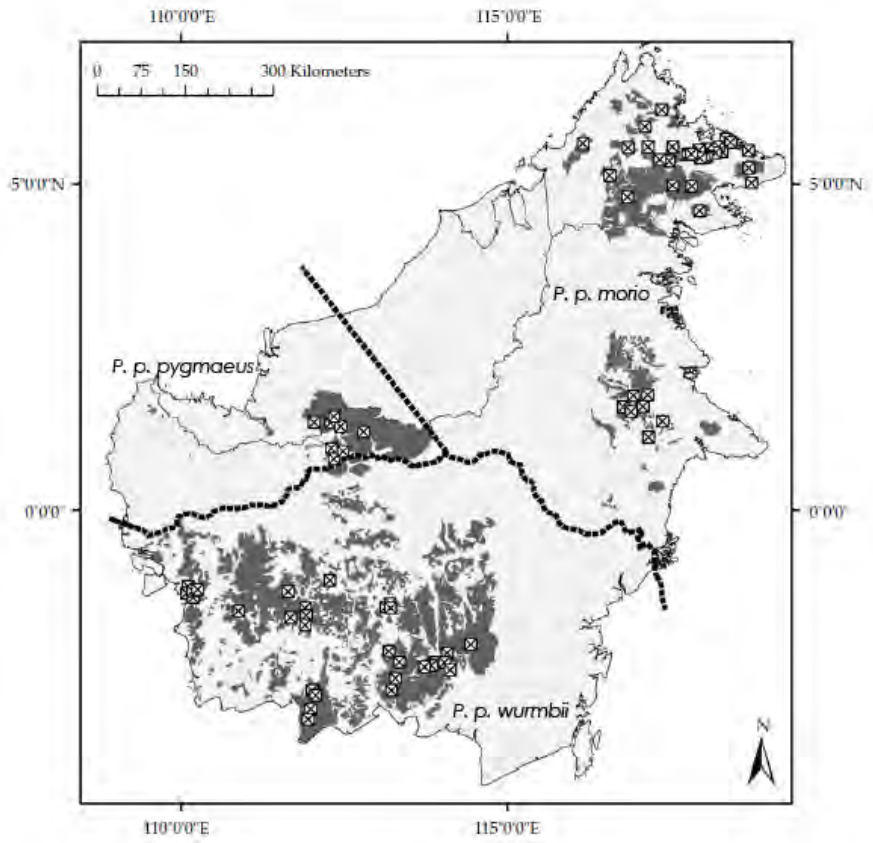
Figure 1.1 – Orangutan Distribution in Sumatra



Taken from Husson et al. (2009), boxed crosses show surveyed locations.

distribution and population structure of Bornean orangutans was shaped by Pleistocene fluctuations as well as sociobehavioural (e.g. male-biased dispersal with female philopatry) and geographical barriers to movement (e.g. large rivers and mountain ranges). Recent mtDNA analysis suggests a radiation of Bornean orangutans in the Middle to Late Pleistocene, with a high differentiation between female "static" clusters (as a result of the smaller dispersal distances of females) separated by geographical barriers, with the more mobile males exerting a homogenising effect on the nuclear gene pool (Arora et al., 2010).

Figure 1.2 – Orangutan Distribution in Borneo



Taken from Husson et al. (2009). Boxed crosses show surveyed locations. Dashed lines mark the boundaries between the three subspecies.

Morphology

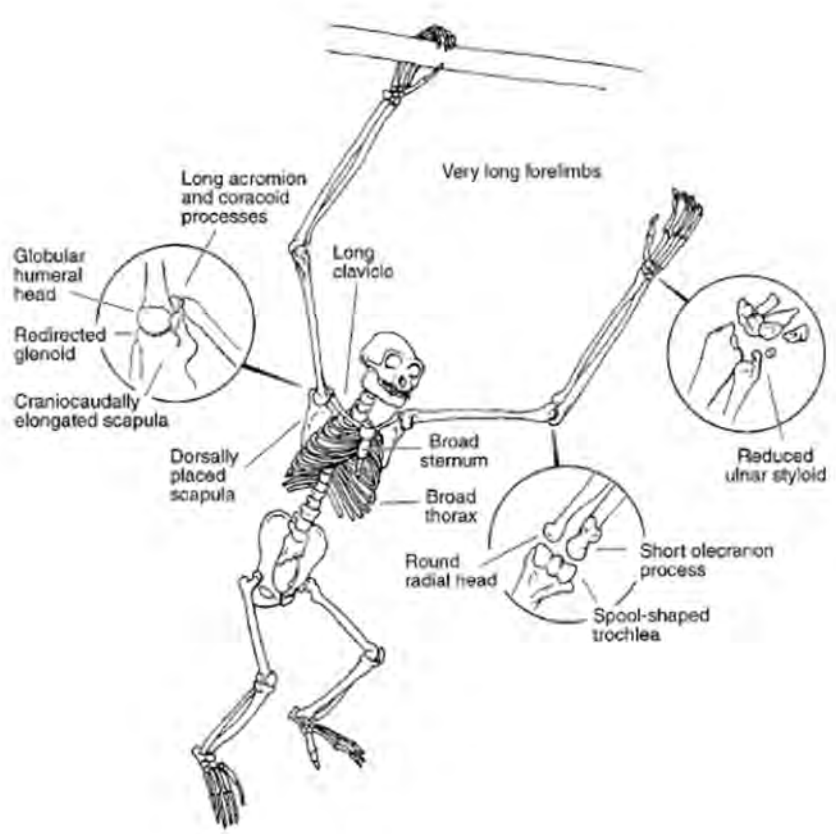
Orangutans are the world's largest living predominantly arboreal primate species (Cant, 1987b). They show extreme sexual dimorphism, adult male orangutans weigh between 80-91kg, more than half that of adult females (33-45kg) (figures are based on Bornean orangutans only. Markham and Groves, 1990). In addition to sexual dimorphism the males also show pronounced bimaturism with two distinct adult morphs (Delgado and van Schaik, 2000; Harrison and Chivers, 2007). Flanged males possess large cheek pads, a large throat sac, are larger than unflanged males, and produce

loud "long calls" to advertise their presence (Rodman, 1973; MacKinnon, 1974; Rijksen, 1978). Unflanged males are generally considered to be about the same size as females, lack the secondary sexual characteristics possessed by flanged males (Galdikas, 1985; Kingsley, 1988) but are sexually mature and can sire offspring (van Hooff, 1995; Maggioncalda et al., 1999; Utami Atmoko, 2000). This pronounced bimaturism is unusual among primates and unique among the great apes (Harrison and Chivers, 2007). The two morphs are thought to represent two alternative mating strategies namely, "call-and-wait" and "sneak-and-rape", with the flanged morph emitting loud long-calls to advertise their presence and are preferred mates by females, whereas the unflanged morphs acquire matings by both harassing females and also by having voluntary consortships with nulliparous females who are perhaps not appealing enough for the dominant flanged males (Harrison and Chivers, 2007; Utami-Atmoko et al., 2009). Whilst unflanged morphs have the ability to develop into flanged morphs, once flanging has occurred it becomes a permanent state.

The living apes share common features for suspension and orthograde climbing, particularly in the trunk and upper limb, such as long forelimbs with a short olecranon process for elbow extension; a broad thorax with deep, narrow dorsally placed scapula to increase reach in all directions, and short lumbar region, to reduce bending of the trunk during suspension and reach; the shoulder complex is directed upwards and the glenoid fossa and humeral head are such to permit a wide range of movement (Ward, 2007; Rose, 1993; 1997; Larson, 1998; Figure 1.3).

The postcranial morphology of orangutans is well adapted for life in the

Figure 1.3 – Shared Commonalities of Living Ape Morphology (form Larson, 1998)



canopy. They have long, highly mobile and powerfully muscled forelimbs (Erikson, 1963; Jungers, 1985b; Schultz, 1936, 1956; Tuttle, 1975). The elongated forearm is thought to be a response to selection for arboreal locomotor behaviour (Schultz, 1933), where the advantages of long forelimbs for suspensory behavior well known (e.g. Jungers and Stern, 1984; Preuschoft and Demes, 1984; Oishi et al., 2008). Certainly elongated forelimbs provide greater reach between arboreal supports (Tuttle, 1975; Preuschoft and Demes, 1985) as well as increased reach during foraging (Grand, 1972). The mid-digits on their hands are curved, elongated and

capable of grasping vines and twigs securely (Tuttle and Cortright, 1988). The wrists of orangutans are highly mobile and the elbow can be fully extended, whilst the shoulder complex is particularly adapted for using the forelimb in upraised positions (Tuttle and Cortright, 1988), which is required for suspensory behaviour as well as reaching (during feeding and also for supports during travel). In comparison to the forelimbs, the hindlimbs of orangutans are very short (Erikson, 1963; Jungers, 1985b) and among the great apes, orangutans have the highest intermembral index (Jungers and Hartman, 1988). Orangutans also have long and powerful feet which are adapted for gripping a wide variety of arboreal supports and highly mobile hip joints that enable a versatile range of positional behaviour. The main muscles of the hindlimbs including the gluteal muscles, flexor (hamstrings) and extensor (vasti) are considered to be well adapted for arboreal locomotion (Payne et al., 2006b). However, orangutans do not differ substantially in their fore- or hindlimb muscle architecture (muscle belly mass, fascicle length or physiological cross sectional area) from other non-human great apes, despite differences in locomotor repertoires, suggesting that the frequency of performing a particular behaviour (e.g. higher levels of suspensory locomotion in orangutans) does not necessarily impose a dominating selective influence on the soft-tissue portion of the musculo-skeletal system (Myatt et al., 2011a, b).

Species Variation

It is estimated that Bornean and Sumatran orangutans diverged between 2.7 – 5 mya (Steiper, 2006). In addition to being genetically distinct, there are a number of morphological and behavioural differences between the two orangutan species, and the higher quality of Sumatran forest in terms of

productivity, compared to Borneo is thought to be both the proximate and ultimate cause of many of these differences (Delgado and van Schaik, 2000; van Schaik, 2004; Marshall et al., 2009). Inter-specific differences have been documented with regard to brain size (Taylor, 2006; Taylor and van Schaik, 2007), craniofacial morphology (Groves and Shea, 1992; Taylor, 2006), dental morphology (Uchida, 1996, 1998), interbirth interval (see review in Taylor and van Schaik, 2007), secondary sexual characteristics (Delgado and van Schaik, 2000) and hair (MacKinnon, 1974). However, interspecific variation with regard to postcranial morphology is not well documented (Thorpe and Crompton, 2009) although the two species are considered to be of similar body size (Markham and Groves, 1990; Smith and Jungers, 1997).

Compared to other body organs, the growth and maintenance of a large brain is metabolically expensive (Aiello and Wheeler, 1995; Isler and Van Schaik, 2006). Thus, the adaptive benefits that ensue from having a larger brain must outweigh the increased energetic costs (Aiello and Wheeler, 1995). The differences in brain size between both the orangutan species and the three Bornean sub-species have been related to differences in forest productivity both between and within the two islands. Orangutans in Borneo have a heavier reliance on hard fallback foods, such as bark, which are stripped from the tree using the teeth (Knott, 1998; Marshall et al., 2009; Harrison et al., 2010). Bornean orangutans have a more robust mandible and thicker tooth enamel than their Sumatran counterparts, and this is considered to be an adaptation for their heavy reliance on bark during periods of fruit scarcity (Taylor, 2006). This difference in mandibular load resistance ability (i.e. the ability to process food with hard mechanical properties) is also observed between the Bornean sub-species as a result of

the increased frequency of periods of fruit scarcity, and therefore heavier reliance on bark as a fallback food from west to east (Taylor, 2006; Taylor and van Schaik, 2007; van Schaik et al., 2009). The Bornean sub-species *Pongo pygmaeus morio* inhabits the least productive habitat, has the lowest energy intake during extended lean periods, has the shortest inter-birth intervals, the most robust mandible and has a significantly smaller cranial capacity compared to most other orangutans groups (Taylor and van Schaik, 2007). In contrast, Sumatran orangutans exist on a fruit dominated diet, as a result of the higher forest productivity, and have the most gracile mandible and a larger cranial capacity, whereas *P. p. wurmbii* and *P. p. pygmaeus* exhibit intermediate levels of frugivory and fall between *P. abelii* and *P. p. morio* in terms of both brain size and mandibular robusticity (Taylor, 2006; Taylor and van Schaik, 2007; Taylor, 2009).

Sumatran flanged males have flatter cheek pads and smaller throat sacs than their Bornean counterparts whose cheek pads point forwards and their throat sacs are larger (Delgado and van Schaik, 2000). In addition, Sumatran orangutans have longer, denser body hair which is lighter in colour than in the Bornean species (MacKinnon, 1974; Delgado and van Schaik, 2000). Sumatran orangutans have a longer inter-birth interval than in Borneo, with the lowest inter-birth interval in the Bornean subspecies *P. p. morio* (Taylor and van Schaik, 2007). Increased brain size has the potential to cause time delays in reaching reproductive age, thus the higher inter-birth interval may be a consequence of the larger brain size in Sumatran orangutans (Ross and Jones, 1999; Taylor and van Schaik, 2007).

Diet and Foraging Strategy

Orangutans are primarily frugivorous (MacKinnon, 1974; Rijksen, 1978) but also feed on leaves flowers, bark, insects and occasionally small mammals (Fox et al., 2004; Wich et al., 2006; Russon et al., 2009; Hardus et al., 2012). Forest productivity has an inverse effect on dietary breadth and intensity of food species use ((Russon et al., 2009). Bornean orangutans consume more families, genera and species than in Sumatra, as well as feeding on more plant parts per species, and eating cambium and leaves from a larger proportion of their plant food species (Russon et al., 2009). There is a west to east gradient in folivory, with the most eastern sub-species (*Pongo pygmaeus morio*) being the most folivorous, whereas the most western species (*Pongo abelii*) being specialised frugivores as they are not normally exposed to long periods of fruit scarcity. The sensitivity of orangutans to selective logging decreases in the same direction and has been attributed to the coping adaptations of eastern populations (larger guts or specialised gut flora and the ability to store fat during periods of high fruit productivity), as folivores are better able to cope with selective logging than specialised frugivores (Meijaard et al., 2007; van Schaik et al., 2009).

Morrogh-Bernard et al. (2009) identified two foraging strategies in orangutans, which correlated with the habitat in which they lived: "sit and wait" where orangutans conserved energy by resting for long periods during fruit scarcity while waiting for periods of high fruiting, this type of strategy is employed in masting forests such as Gunung Palung; and "search and find" where orangutans continually feed and travel in search of food, and occurs where there is a constant supply of food, but which is generally of a lower quality, for example in peat-swamp forests such as Suaq

Balimbing and Sabangau.

Fallback foods are regarded as foods of poorer nutritional quality, yet high abundance and are eaten when preferred foods are unavailable (Knott, 1998; Marshall and Wrangham, 2007; Marshall et al., 2009; Harrison and Marshall, 2011). The consumption of fallback foods is considered to have important influences on primate biology, particularly in shaping morphological adaptations, behaviour and socioecology (see review in Marshall and Wrangham, 2007). Orangutans have high molar shearing crests, high molar-surface slopes and steep molar-cusp slopes which facilitate the efficient breakdown of structural carbohydrates during mastication (i.e., leaf eating, Kay, 1977, 1981; Ungar, 2006). They also have a large gut and slow passage rate (Kay, 1981). These traits suggest adaptations for dealing with difficult-to-process fallback foods.

1.3 Orangutan Habitat

Forest Productivity

Orangutan habitats vary with regard to food abundance (Delgado and van Schaik, 2000). However, it is generally accepted that forest productivity is higher in Sumatra than in Borneo regardless of forest type. Sumatra's younger, predominantly volcanic soils are more fertile than Borneo's older, more weathered soils (MacKinnon et al., 1996; Rijksen and Meijaard, 1999; Marshall et al., 2006; Wich et al., 2011). Fruit production in three forest types (dryland, riverine, and peat-swamp) was found to be significantly higher in Sumatra than in Borneo (Wich et al., 2011). The amount of fruit in the diet of orangutans is much less temporally variable in Sumatra than in Borneo

(Wich et al., 2006) and orangutans occur at higher densities and are more sociable as a result of higher quality forest. Field studies have also shown that in Borneo orangutans occasionally experienced relatively extreme periods of negative energy balance, indicated by the excretion of ketone bodies in urine signifying the metabolism of fat stores (Knott, 1998; Harrison et al., 2010), while those in Sumatra did not (Wich et al, 2006).

Peat-Swamp Forests

In South-East Asia the majority of peat soils developed in or near coastal plains as early as 30 000 BP (Page et al., 2004) and the total area covered by peat swamps in South East Asia is estimated to be approximately 33 million ha (RePPProT, 1990), of which 82% is located in Indonesia. Poor drainage, permanent waterlogging, high rainfall and substrate acidification produce conditions whereby plant residues accumulate faster than they decay (Brady, 1997). Lowland tropical peat is comprised mainly of partially decomposed tree trunks, branches and tree roots within a matrix of almost structureless organic material that also originates from rainforest plants (Rieley et al., 1996).

The lowland peat-swamp forests of South-East Asia form extensive, gently-domed deposits, which can extend up to 200km inland and reach thicknesses of up to 20m (Anderson, 1983; Whitten et al., 2000; Page et al., 2004). Peat-swamp forests comprise a sequence of forest types replacing each other from the edge to the centre of the dome (Anderson, 1983; Brady, 1997; Stoneman, 1997; Page et al., 1999). With the exception of shallow peats around the periphery which are subject to tidal or riverine inundations, the only source of nutrients to these forests comes from aerial precipitation (rain

and, to a lesser extent, dust). That the vast majority of nutrients come from rainfall makes these peatlands ombotrophic ("cloud-fed"), although there is small nutrient input from nitrogen fixation by micro-organisms (Jordan, 1985; Wild, 1989), and fauna migration through animal faeces (Sturges et al., 1974). These ombotrophic peatlands are acid, nutrient-poor, subject to seasonal or permanent water-logging, and, although they support a lower diversity and density of flora and fauna than dryland rain forests, contain a large number of endemic species and are recognised as important reservoirs of biodiversity (Whitmore, 1975; Prentice and Parish, 1990; Page et al., 1997; Shepherd et al., 1997).

Peat-swamp forest provides a home for five out of eight of the world's largest remaining populations of wild orang-utans, comprising possibly a third or more of the total Bornean population (Meijaard, 1997; Singleton et al., 2004). Peat-forming wetlands act as important carbon sinks, with between one-fifth and one-third of global soil carbon locked up in their soils (Gorham, 1991). As a result of the large amount of carbon stored in their soils, the stability of tropical peat swamps has major implications for global climate. Forest fires, brought about as a result of dry peat conditions, due to the effects of the El Niño-induced drought as well as peat drainage from illegal logging canals, caused the release of huge amounts of carbon in 1997, which contributed to the largest annual increase in global atmospheric CO_2 concentrations since records began in 1957 (Page et al., 2002). Therefore, the preservation of tropical peatlands is of paramount importance, both locally and globally.

Dry lowland Forest

Lowland forests of Southeast Asia are mainly dominated by trees of the family Dipterocarpaceae. These are the only forests in the world where a single family has such a high density of genera, species, and individuals (Whitmore, 1984). However, there are other types of lowland forests including Heath forest (*Kerangas*), alluvial forest, which has some of the most luxuriant of all plant communities (Proctor et al., 1983), and ironwood and limestone forests. The rainforests of Southeast Asia have had a long and relatively stable history, and whilst the area covered by rainforests may have expanded and contracted several times during the Pleistocene, they were essentially unchanged in character and composition (MacKinnon et al., 1996).

The lowland forests of Sumatra and Borneo have an extremely high diversity of tree species and the large number of animal species is generally associated with the structural and taxonomic heterogeneity of the plants (MacKinnon et al., 1996; Whitten et al., 2000). Soil texture, levels of iron and aluminium oxides and the acidity of the soil parent material have been identified as important factors in determining species composition and particularly species density (Baillie and Ashton, 1983). Whilst dipterocarp trees dominate most lowland rainforests in the region, other families may be dominant or have equal dominance with the dipterocarps, such as Myristicaceae, Euphorbiaceae, Sapotaceae and Meliaceae.

Lowland forests are characterised by the conspicuous presence of thick lianas, trees with large buttresses and the prevalence of trees with tall, smooth-barked trunks (Whitten et al., 2000). Dry lowland forests have a tall

canopy, with the top of the canopy reaching around 45 m (Whitmore, 1984), with emergent trees in both Sumatran and Bornean lowland forest reaching as much as 60 - 70 m tall (MacKinnon et al., 1996; Whitten et al., 2000). These emergents generally belong to the family Dipterocarpaceae and Caesalpiniaceae (e.g. *Koompasia*).

Mast fruiting is the simultaneous mass fruiting of certain trees over wide areas and takes place approximately every 2-10 years (Ashton et al., 1988). This phenomenon is only found in the forests of Southeast Asia and is particularly associated with the Dipterocarpaceae although up to 88% of all canopy species can produce fruit after years of reproductive inactivity (Medway, 1972; Appanah, 1981; van Schaik, 1986; Whitten et al., 2000). Thus, despite no seasonal change in temperature and little variation in rainfall, the rainforests of Southeast Asia are characterized by substantial fluctuations in fruit production. In addition to supra-annual mast fruiting events, annual fruit peaks also occur (Knott, 1998). This seasonal change in fruit availability has been linked to significant vertebrate migrations (Leighton and Leighton, 1983) as well as primate reproductive patterns (van Schaik and van Noordwijk, 1986).

1.4 Orangutan Evolution (Palaeontology and Functional Anatomy)

Proconsul species date from the Early and Early Middle Miocene (c. 20-17 Ma) and are the first Mioecene apes described from Africa (Hopwood, 1933). Proconsul species range in size from around 11 kg for *P. heseloni*, to 35.6 kg for *P. nyanzae* to as large as 75 kg for *P. major* (Rafferty et al., 1995;

Walker, 1997) although *P. major* is known only from a few remains (Fleagle, 1999; Crompton et al., 2008). Proconsul species were associated with evergreen tropical forests, or environments similar to the present day coastal forests of Kenya (Andrews and Humphrey, 1999; Crompton et al., 2008). The skeleton of *P. heseloni* has limb proportions more similar to those of living cercopithecids rather than living hominoids, indicating this species was quadrupedal, and most likely arboreal, similar to the locomotor behaviour of present day cercopithecids, but with higher frequencies of climbing, yet lacking the suspensory abilities of the living hominoids (Pickford, 1983; Rose, 1993, 1997). Computer modelling of *P. heseloni* has shown that the limb proportions best match the quadrupedal gait of macaques (Li et al., 2002) and the morphology and proportions of the fossil hand bones also indicates that Proconsul was a predominantly above-branch, palmigrade quadruped with powerful grasping abilities (Ward, 1993; Walker, 1997). Thus a short hand with a relatively long thumb is considered to be the primitive condition from which the elongated hands of the orthograde living apes must have evolved (Almécija et al., 2007).

Pierolapithecus dates from the Middle Miocene (13.0 – 12.5 Ma) and its body weight is estimated to be around 34 kg, similar to that of *Hispanopithecus (Dryopithecus) laietanus* (Moyà-Solà et al., 2004; Crompton et al., 2008). Discovered in 2002 in Catalonia, Spain, the remains of the postcrania of *Pierolapithecus* indicate this Miocene ape had an orthograde bodyplan (Moyà-Solà et al., 2004, 2005). Whether *Pierolapithecus* had suspensory adaptations is a matter of debate, Moyà-Solà et al. (2004) suggested that the short phalanges indicate that there was no substantial suspensory behaviour, whereas Begun and Ward (2005) dispute that, instead suggesting

that the curvature of the phalanges indicates that there was a suspensory component to the locomotor behaviour of Pierolapithecus. Whilst the postcrania of *Pierolapithecus* indicates a unique positional behaviour repertoire (Moyà-Solà et al., 2005; Begun and Ward, 2005). Begun and Ward (2005) suggest that fossil evidence indicates the inclusion of climbing and suspension with a limited amount of palmigrady and changes seen in later hominoids may signify further specialisation for forelimb-dominated below-branch arboreality combined with large body size and the abandonment of palmigrady.

Dryopithecus, a late Miocene ape, is probably the most well-known European fossil ape. However, recent analysis of craniodental and postcranial remains has revealed that the Dryopithecines are more diverse at the genus level than originally thought (Begun et al., 2008). The fossil hominine from Can Llobateres in Spain, described for a long time as *Dryopithecus laietanus* (Moyà-Solà and Köhler, 1996; Kohler et al., 2001) is now considered a separate genus *Hispanopithecus laietanus* (Begun, 2002; Almécija et al., 2007) and the fossil hominine from from Rudaba´nya, Hungary, previously assigned to the taxon *Dryopithecus brancoi* (Begun and Kordos, 1993) is now classified as *Rudapithecus hungaricus* or *Hispanopithecus hungaricus* (Begun et al., 2008).

Hispanopithecus laietanus (9.5 Ma) are late Miocene great apes known from a number of localities within the Valles-Penedes in Catalonia, Spain (Begun et al., 1990; Moyà-Solà and Köhler, 1996; Almécija et al., 2007; Alba et al., 2012). It is estimated to have a body mass of around 34 kg, similar to that of present day female orang-utans (Crompton et al., 2008; Smith and Jungers,

1997). The postcranial skeleton of *H. laietanus* indicate an orthograde body plan with a wide and shallow thorax (Moyà-Solà and Köhler, 1996). The relative limb proportions of *H. laietanus* are more similar to orangutans than African apes, with very long forelimbs and short femora (Moyà-Solà and Köhler, 1996; Köhler et al., 2002; Pina et al., 2012). The morphology of the hand of *H. laietanus* indicates powerful grasping capabilities as well as ensuring enhanced resistance against lateral stresses during climbing and/or suspension, further providing a secure and powerful grasp during palmigrade quadrupedalism (Almécija et al., 2007). The hand morphology indicates that palmigrade quadrupedalism was combined with orthogrady, below-branch suspension, arm-swinging, clambering and postural feeding on slender arboreal supports facilitated by an orangutan-like double-locking mechanism (Almécija et al., 2007; Crompton et al., 2008). Crompton et al. (2008) suggest that *H. laietanus* were most likely habitually orthograde, whether in suspension or compression, and also capable of pronograde suspensory locomotion. The robusticity of metacarpals depends to a large extent on their length relative to body mass and that orangutans have the longest and least robust metacarpals has been ascribed to the lack of habitually supporting weight-bearing compressive stresses (Almécija et al., 2007). The metacarpals of *Hispanopithecus* more closely resemble orangutans than the metacarpals of *Sivapithecus* indicating a higher significance of palmigrady at the expense of suspensory behaviours in *Sivapithecus*. *Hispanopithecus*, interpreted as either an early pongine (Moya-Solà and Köhler, 1993, 1995; Kohler et al., 2001) or hominine (Begun et al., 1997), represents the first simultaneous evidence in the hominoid fossil record of an orthograde bodyplan coupled with suspensory adaptations (Almécija et al., 2007).

Rudapithecus, is another Eurpean late Miocene ape and has a body mass between roughly 20–40 kg suggesting a large degree of sexual dimorphism similar to that of extant *Pongo* or *Gorilla* (Morbeck, 1983; Begun, 1994; Kivell and Begun, 2009). Postcranial remains indicate that the positional behavior of *Rudapithecus* included suspension, climbing, and some quadrupedalism (Morbeck, 1983; Begun, 1988, 1992, 1993, 1994; Kivell and Begun, 2006). The morphology of *Rudapithecus* is similar to suspensory and brachiating hominoids, particularly *Pongo* although in many aspects it appears to have a more generalised arboreal-hominoid morphology (Kivell and Begun, 2006). The functional morphology of the wrist (scaphoid and capitate) is hominoid-like and consistent with arboreal locomotion, including more suspensory and climbing activities than is typical of arboreal or terrestrial monkeys and appears to have a large degree of mobility consistent with the functional interpretation of other postcranial remains from this taxon (Begun, 1988, 1992, 1993, 1994; Kivell and Begun, 2006). Thus *Rudapithecus* is considered to be an arboreal ape, capable of more suspension, climbing, and quadrupedalism than the early Miocene hominoids yet lacking all the distinct locomotor specialisations of any one extant hominoid taxon (Kivell and Begun, 2009). Begun (1992) suggests suspensory quadrupedalism was practiced by both *Rudapithecus hungaricus* and *Hispanopithecus laietanus* (Begun et al., 2008) which is interesting as of the extant great apes, only the orangutan exhibits this behaviour (Thorpe and Crompton, 2006). However, Crompton et al. (2008) correctly note that the absence of suspensory quadrupedalism in panines and gorillines may be a statistical consequence of greater arboreality in *Pongo*.

Sivapithecus from the Siwalik Hills of Pakistan and Northern India (9 to 12

Ma). The skulls of *Sivapithecus* strongly resemble the living orangutan, having a narrow snout. Although skeletal remains of the postcrania are limited, most indicate that *Sivapithecus* lacked the extreme adaptations for suspensory locomotion found in *Pongo*. *Siviapithecus* was likely to be more quadrupedal, although the large range in body size of the *Sivapithecus* species indicate that there was considerable locomotor diversity within the genus. The late Miocene specimens of *Sivapithecus* (c. 9-12 Ma) and the living *Pongo* are extremely similar in many details of dental and facial morphology and *Pongo* is generally considered to have derived from *Sivapithecus* (Kappelman et al., 1991). However, based on differences of skeletal anatomy, particularly with regard to the proximal shaft of the humeri, between *Sivapithecus* and *Pongo* this link has been put into question (e.g. Pilbeam et al., 1990; Pilbeam, 1996). Pilbeam et al. (1990) suggest that if *Pongo* and *Sivapithecus* are sister taxa, suspensory adaptations arose in parallel in African apes and *Pongo*, or that, if they are not sister taxa the palatal and facial similarities between *Pongo* and *Sivapithecus* must themselves be homoplastic. Forelimb suspension is not a predominant locomotor mode of the great apes (Thorpe and Crompton, 2006), and fossil evidence for early crown hominoids suggest that it was not a predominant element of the crown hominoid locomotor niche (Crompton et al., 2008).

Precise dating of the divergence of the orangutan lineage from that leading to African apes and humans is complicated as there is speculation as to whether similarities between the extant orangutans and *Sivapithecus* are specialisations unique to only the latest *Sivapithecus* species, or remnants of the primitive hominoid morphology that characterises the ancestors of all extant apes and hominids. Molecular studies have indicated dates of 10

million to 12 million years ago for the orangutan divergence, all concordant with the fossil data (Fleagle, 1999). The geographic and temporal gap between the late Miocene fossils and the present day orangutans of Borneo and Sumatra is partly bridged by fossil teeth from the Pleistocene of China and Java, however, the lineage leading to extant orangutans is thought to have once contained a greater diversity of species (Fleagle, 1999).

1.5 Positional Behaviour

Primate Positional Behaviour

The study of positional behaviour encompasses both locomotion and posture. By definition, posture is a state where the centre of mass remains broadly static relative to the surroundings, although minor adjustments of limbs may occur, whereas locomotion is the action of moving from one place to another therefore involving a gross mass displacement (Prost, 1965). Primate field research substantially increased in the 1960's, and whilst studies of animal locomotion extend as far back as the end of the 19th Century with Muybridge's book on animal locomotion (1899), field studies investigating morphological patterns were relatively uncommon (e.g. Ripley, 1967; Mendel, 1976) until the work of Fleagle and colleagues (1974; 1976; 1978; 1980; 1981) see review in Rodman and Cant (1984). Indeed Fleagle and colleagues are considered pioneers in combing both field and laboratory research on primate locomotion (e.g. Fleagle 1974; 1976; 1988; 1988; 1999; 1999; Fleagle and Mittermeier, 1980). Rodman and Cant's (1984) book on adaptations in foraging behaviour highlights the importance of examining the relationship between form and function in a natural setting with chapters examining how structure and behaviour effect solutions to the

same problem (Grand, 1984) and the interactions of primates with their microhabitats (Crompton, 1984; . Field primatologists have undertaken studies of positional behaviour since the 1960s (e.g. Napier and Napier, 1967; Richard, 1970; Grand, 1972; Rose, 1973, 1976; Chivers, 1974; Mittermeier and Fleagle, 1976; Mittermeier, 1978); with in-depth biomechanics research of primate locomotion being studied as early as the 1930s (Elftman and Manter, 1935, see review in Vereecke and D'Aout, 2011). Studies of positional behaviour in the wild are important as they provide a critical link between ecology, behaviour, and morphology, hence the justification for many positional behaviour field studies has been the need to quantify behaviour in order to understand the functional significance of morphological traits (Cant, 1992; Stafford et al., 2003).

Although primates spend more time in posture than in locomotor behaviours, the higher forces generated during locomotion are likely to have a greater influence on the locomotor system than those associated with posture (Hunt, 1991). However, not all locomotor behaviour in the repertoire of a species will drive morphological change, rather, those behaviours which encounter the most stresses, or sub-maximal stresses regularly, will most likely drive morphological modifications over time, which in turn improve overall performance capability (Preuschoft, 1979; Hunt, 1991; Hunt et al., 1996). These behaviours may be frequent, or rare, but key to performance success. Muscle tissue, tendons and bones are adapted to cope with all stresses experienced within a species' repertoire as any behaviour exceeding such a threshold would result in the failure of that structure, which could result in injury or even death (Preuschoft, 1979; Biewener, 2003).

Primates are notable in their positional behaviour as the majority are arboreal and have diverse strategies for negotiating the complex three dimensional environment in which they live (Blanchard and Crompton, 2011). The Primate order is also extremely diverse in terms of body size, ranging from Berthe's mouse lemur (*Microcebus berthae*) with a mass of around 30 g, to male gorillas (*Gorilla* spp.), with a body mass of around 200 kg (Zihlman and McFarland, 2000; Dammhahn and Kappeler, 2005). The positional behaviour of arboreal primate species is both constrained and facilitated by body size and anatomical traits, which have evolved in parallel contributing to solutions for environmental problems (Cant, 1992; Garber and Pruetz, 1995; Dagosto and Gebo, 1998). Nevertheless, the challenges associated with negotiating a complex arboreal environment are amplified with increasing body size and classic theories predict a direct correlation between increased levels of suspension with increasing body mass (Cartmill and Milton, 1977), since as support diameter decreases or body mass increases it becomes more difficult to maintain balance atop a support, whereas suspension enhances stability, as the animal has, in effect, already fallen off (Cartmill, 1985a). However, a number of studies have shown that the positional behaviour of arboreal primates does not always conform to theoretical predictions based on body size (e.g. Gebo and Chapman, 1995; McGraw, 1998; Thorpe and Crompton, 2005; Thorpe et al., 2009).

Almost 50 years ago, Prost (1965) highlighted the necessity for a standardised system to compare positional behaviour. However, only in relatively recent years has the standardisation in the classification of primate positional behaviour (Hunt et al., 1996) provided a foundation for

comparative studies of positional behaviour. These classifications are based on the number of weight bearing limbs, with the body part bearing the most weight recorded first in the definition. Whether limbs are suspensory or in compression, flexed or extended as well as the orientation of the body (orthograde or pronograde) are also important aspects of the classification procedure (Hunt et al., 1996). These standardised descriptions have undoubtedly provided an important contribution to the study of the positional behaviour of primates.

Dagosto and Yamashita (1998) correctly note that only through the determination of the full extent of intraspecific variation in primate positional behaviour, can the importance of interspecific variation be properly assessed. Previous studies on arboreal primates have shown that intraspecific variation in positional behaviour can exist due to factors such as body size, habitat structure, social rank, season and the distribution and availability of resources (Crompton, 1983, 1984; Gebo, 1992; Doran, 1992, Doran, 1993a; Gebo and Chapman, 1995; Dagosto, 1995). Seasonal differences in observed behaviour have been attributed to the structural features of the resources being exploited at that particular time which require different foraging techniques (Crompton, 1984; Dagosto, 1995; Youlatos, 2008).

Studies investigating the influence of habitat structure on arboreal primates have had varied results and it is clear that not all primate species respond in the same way to variation in habitat structure. It is likely that the level of contrast between habitat types will affect the amount of influence on positional behaviour since certain habitat features may matter to a greater or

lesser extent in different species. Forest structure had only a minor influence on the locomotor behaviour of moustached tamarin monkeys (*Saguinus mystax*), although they used different supports in different forest types (Garber and Pruetz, 1995). The locomotor behaviour of five cercopithecid species also remained constant in structurally different forests and this was ascribed to the selection of the same preferred supports in different forest types (McGraw, 1996). In contrast, the positional behaviour of red colobus monkeys (*Colobus badius*) varied between forest types, particularly with regard to the frequency of quadrupedalism and leaping (Gebo and Chapman, 1995). Similarly, the positional behaviour of three species of lemur also differed between two forest types, and although the degree of change differed between the three species studies, their behaviour altered in a similar direction, and all three species leaped more and moved quadrupedally less in forest with a lower stature, thinner trunks and a less developed canopy (Dagosto and Yamashita, 1998).

Orangutan Positional Behaviour

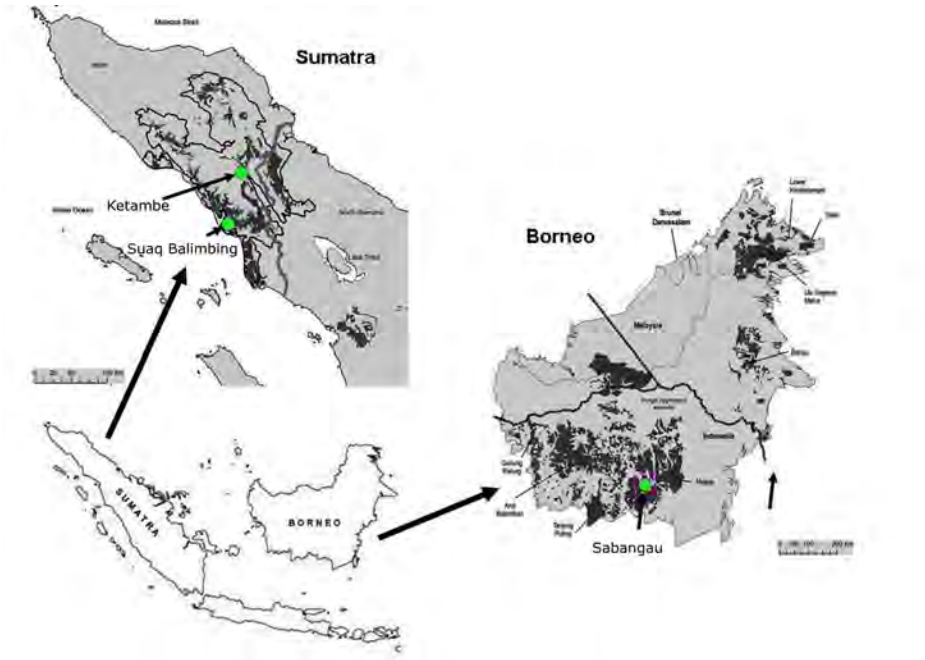
The Asian apes, more than any other, are restricted to an arboreal habitat (Thorpe and Crompton, 2006). Studies of the positional behaviour of orangutans (*Pongo* spp.) are interesting not least because they are the world's largest predominantly arboreal primate (Cant, 1987a). Early studies of orangutan locomotion tended to be qualitative rather than quantitative (see review in Tuttle and Cortright, 1988). Sugardjito (1982) was the first to quantify the locomotor behaviour of Sumatran orangutans (*P. abelii*). However, his study combined locomotor modes into only a small number of categories and only presented frequencies for locomotion during travel on adult males and adult females. A more detailed study at the same site

(Sugardjito and van Hooff, 1986) followed including both posture (whilst resting) and locomotion for all age-sex classes as well as including information on height of the animal in the canopy. However, details on feeding behaviour were not included in the study and no data was presented for support use, other than for lying down. In addition, posture was divided into only four categories and locomotion into five categories. Cant (1987b) was the first to undertake a study of the locomotor behaviour of Bornean orangutans (*P. p. morio*). However, this study only involved two adult females and took place during an "el niño" year, which may have influenced the ranging and foraging patterns of his subjects (Thorpe and Crompton, 2006). Whilst Cant's study (1987b) also grouped locomotor modes into only a few categories, it did include data on both support type and support diameter, although this was only for the main weight bearing support. Crucially it also included information on the orientation of the torso, which is fundamental for understanding the relationship between positional behaviour and morphology. More recently, Thorpe and Crompton (2005) carried out a detailed study of the locomotor behaviour of *P. abelii* including detailed information on height, support type, support diameter and contextual behaviour for all age-sex classes. The primary result from this study was that support diameter (which reflects support compliance as smaller supports are more flexible), followed by support type (both weighted by the number of weight bearing supports), had the greatest influence on orangutan locomotion. This comprehensive study enabled a comparison both between the two orangutan species and also allowed for a comparison between orangutans and other hominids, and provided detailed classifications of orangutan positional behaviour, following Hunt et al.'s (1996) framework (Thorpe and Crompton, 2006).

The large body size of orangutans, coupled with their arboreal lifestyle, has been the basis for recent studies investigating the effects of support compliance on orangutan locomotion (Thorpe et al., 2007a, b, 2009). Orangutans are notable in their ability to tree-sway, where they are able to cross gaps in the canopy by oscillating a flexible support back and forth until the amplitude of the oscillations is sufficient to reach supports on the other side of the gap (Chevalier-Skolnikoff et al., 1982). Thorpe et al. (2007b) showed mathematically that sway actually reduced the energetic cost of crossing a gap when compared to either jumping across the same gap, or descending the tree, crossing terrestrially and then climbing on the other side of the gap. In addition to utilising compliant supports for gap crossing via tree-sway, orangutans have also been found to employ unique strategies to cope with the smallest, most compliant supports; such as hand assisted bipedalism, which enables progression on small supports, typical of the terminal branch niche as it lowers the body's centre of mass (due to the short hindlimbs), whilst keeping the forelimbs free to aid with balance and reach (Thorpe et al., 2007b). Orangutans also cope with small supports by using a mixture of orthograde and pronograde behaviour together with a slow and irregular gait, which helps to reduce the oscillations of supports (Thorpe et al., 2009).

The locomotor behaviour of orangutans is predominantly orthograde suspension whereby the body is orthograde with the head superior, and various combinations of all four appendages grasp supports in different ways, with suspension by the forelimbs from above (Thorpe and Crompton, 2005; Cant, 1987a). The use of orthograde postures in general, both in suspension and compression, characterise the positional behaviour of the

Figure 1.4 – Study Sites



non-human apes (Thorpe and Crompton, 2006; Crompton et al., 2008). All apes are adapted to suspensory postures, and commonalities of their morphology include the ability to completely abduct the humerus and wide range of scapular motion (Hunt, 1991; Pilbeam, 1996) with suspensory positional behaviour observed in all non-human apes (e.g. Hunt, 1992; Doran, 1993a; Remis, 1995; Fleagle, 1999; Thorpe and Crompton, 2006). However, pronograde suspension is a behaviour thought to be unique among living apes to orangutans. This suggests that adaptations for pronogrady evolved in parallel in orangutans and the African apes, but had different forms with orangutans developing both suspensory and compressive pronogrady, but the African apes only developing compressive pronogrady as a result of their predominantly terrestrial nature (Thorpe and Crompton, 2006; Thorpe et al., 2009).

Positional behaviour underlies the success of all foraging and predator avoidance strategies which ultimately lead to reproductive success (Cant, 1992). The type of foraging strategy employed by orangutans has been linked to fruit productivity (Morrogh-Bernard et al., 2009). In the Sabangau, Suaq Balimbing and Ketambe (i.e. sites used in this study) orangutans employ a "search and find" foraging strategy whereby individuals spend more time feeding and travelling in search of food in order to maintain their daily metabolic requirements (Morrogh-Bernard et al., 2009). Whilst orangutans spend almost all of their time in the canopy, they do sometimes travel on the ground. This behaviour is more commonly observed in Bornean orangutans where adult males, in particular, can travel for long periods on the ground (MacKinnon, 1974; Galdikas, 1979; Rodman, 1979a; Tuttle, 1986; Rodman and Mitani, 1987; Manduell, personal observations) although both juvenile and females are also known to travel on the ground over short periods (MacKinnon, 1974; Manduell, personal observations). Cant (1987a) attributes this major difference in habitat use between Bornean and Sumatran orangutans to the predator avoidance, given the presence of tigers (*Panthera tigris sumatrae*) in Sumatra, whereas in Borneo there are no predators sufficiently large to threaten adult orangutans.

Whilst the study of orangutan positional behaviour has progressed in recent years, it must be noted that all previous studies of were undertaken in dry lowland forest, with the majority being undertaken at one field site in Sumatra (e.g. Sugardjito, 1982; Sugardjito and van Hooff, 1986; Cant, 1987a; Thorpe and Crompton, 2005, 2006, 2009; Thorpe et al., 2007a, b, 2009; Myatt and Thorpe, 2011). Thus, there remains a gap in our understanding of positional behaviour of wild orangutans and how this may differ between

species and how it may be affected by habitat variation.

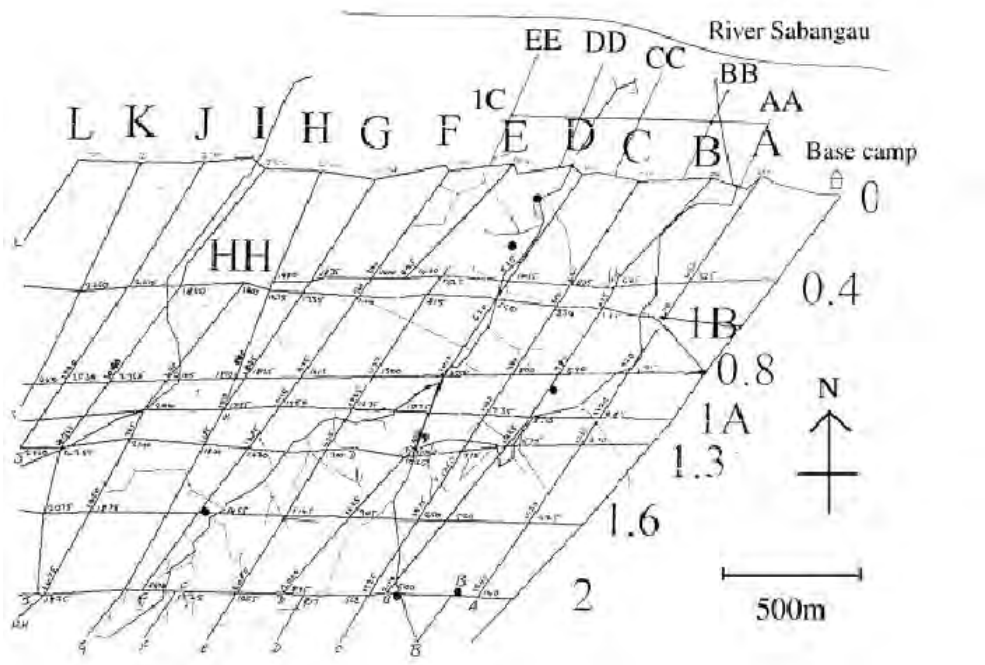
1.6 Study Sites

Sabangau

Sabangau research site (Figure 1.4) is in the Natural laboratory of peat-swamp forest (NLPSF) in the Sabangau Ecosystem, Central Kalimantan (21° 31′ S, 113° 90′ E). At around sea level the site receives a mean annual rainfall of 2,790 mm and has a distinct wet and dry season. The Sabangau Catchment is bordered by the Kahayan River to the east, and the Katingan River to the west. Research on the orangutan sub-species *Pongo pygmaeus wurmbii* began in the NLPSF in 2003 and continues today. The area is managed by the Centre for the International Cooperation in Management of Tropical Peatlands (CIMTROP). The NLPSF occupies an area of 500 km^2, thus comprising only a small proportion of the total 9,200 km^2 of forest in Sabangau (Morrogh-Bernard, 2003).

The area was a logging concession from 1966 through to 1996, following which illegal logging became widespread. However, illegal logging has been eliminated in the NLPSF since 2004. The area has also suffered from major fires in 1997-1998, 2001-2002, and 2006-2007. The creation of canals to transport timber out of the forest has had an enormous detrimental impact. Drainage of the peat has lowered the water table, which has led to decreased stability of the peat, and has increased the frequency and severity of fire and the risk of peat collapse, in fact, these two factors are now considered to be major threats to orangutan populations in the area (Singleton et al., 2004; Wich et al., 2008).

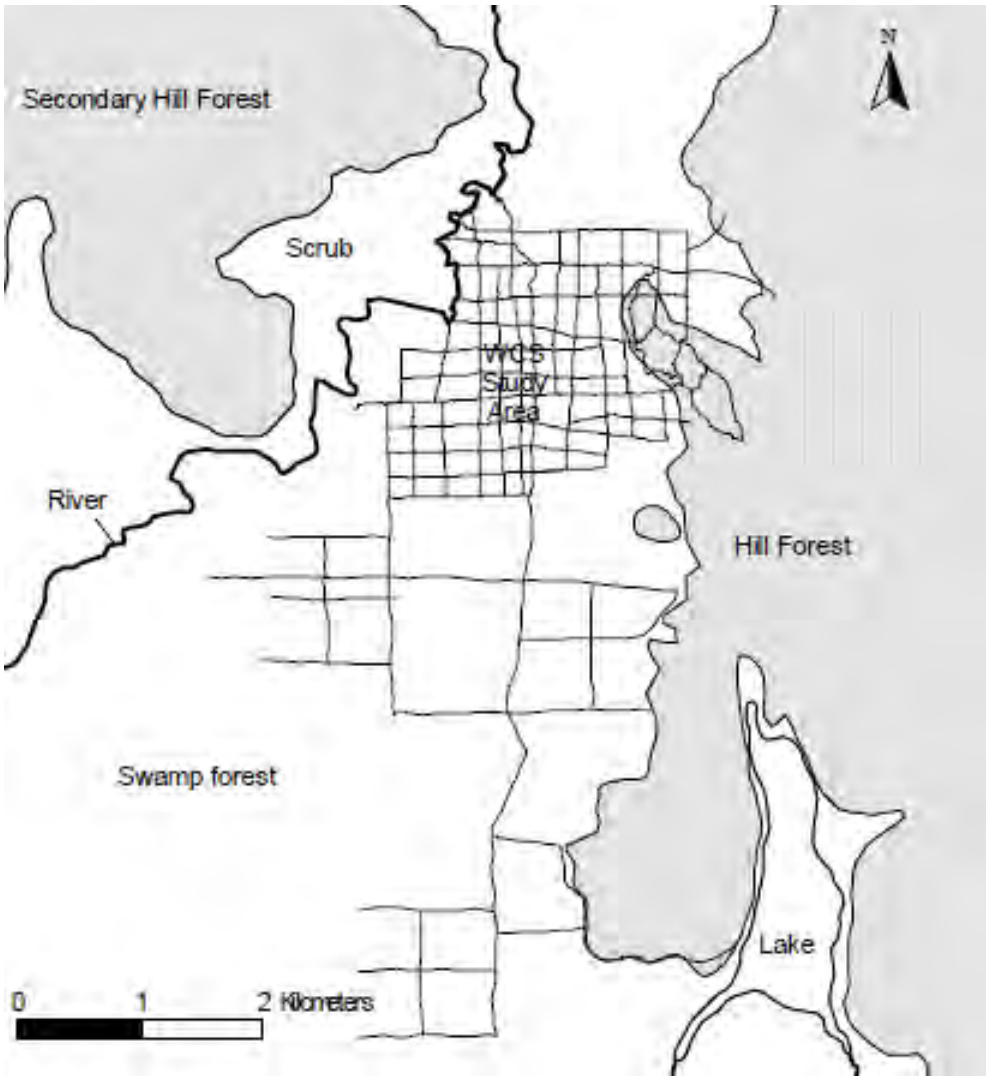
Figure 1.5 – Sabangau Grid System



The NLPSF is a fully ombrogenous peat-swamp forest as the only nutrient input is through rainfall (Shepherd et al., 1997). Four main habitat sub-types have been identified: mixed-swamp forest, around 0-4 km from the river; low-pole forest, around 6-11 km from the river; tall-pole forest, from around 12 km from the river on the most elevated part of the peat dome (Harrison, 2009c); and low canopy forest in the very centre of the peat dome. Orangutan behavioural research is conducted in the area of mixed-swamp forest in a 2 x 2 km^2 grid system (Figure 1.5)

Although the Sabangau catchment is home to the largest contiguous orangutan population, thought to number around 6,900 individuals (Morrogh-Bernard et al., 2003; Singleton et al., 2004; Wich et al., 2008), densities are lower here than in Sumatran peat-swamp forest as a result of

Figure 1.6 – Suaq Balimbing Grid System



the lower productivity Bornean forests and number around 2.35 ind/km^2 (standardised densities, Husson et al., 2009).

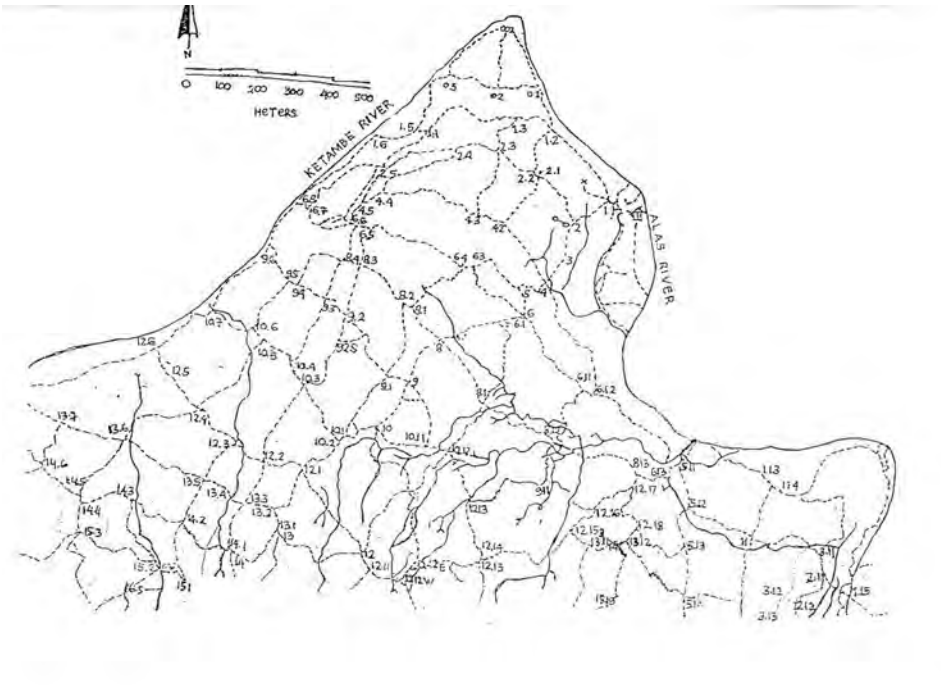
Suaq Balimbing

Suaq Balimbing research site (Figure 1.4) is situated in the Kluet region in the western coastal plain of the Leuser Ecosystem (3° 42′ N, 97° 26′ E) at around sea level, and experiences two wetter and two drier periods with a

mean annual rainfall of 3,400 mm (Wich et al., 2009). The Kluet region lies within the district of South Aceh, between the Barisan mountains and the coast. The majority of the Leuser Ecosystem falls within the province of Aceh, Sumatra, but also straddles the border to the south, into the province of North Sumatra (Singleton, 2000). The site was established in 1992 and research on the Sumatran orangutan (*Pongo abelii*) was conducted there through to 1999, when it had to be halted due to the unstable political situation in Aceh. The site was however reopened in 2007 (Wich et al., 2009).

The study area at Suaq Balimbing is bordered to the west by the Krueng Lembang River, and to the east by low hills (reaching 500 m). Within the area four main habitat types have been identified: 1) tall riverine forest along the Krueng Lembang River (floodwater pH 6-7); 2) regularly flooded 'backswamps' near the river and foothills, on muddy soils with a very irregular and open forest (floodwater pH 5-6.5); 3) structurally simple, but generally closed canopy peat swamp forest , in which the peat layer becomes deeper away from the backswamps (floodwater pH 3.5-5.5); 4) mixed dipterocarp hill forest (van Schaik, 1999; Singleton, 2000). Large strangling figs (*Ficus* spp.) are virtually absent except for a very few, widely scattered trees, even in the hill forest (Singleton, 2000). However, forest productivity is high in Suaq Balimbing and as a consequence orangutans occur at high densities with a standardised estimate of 7.44 ind/km^2 (Husson et al., 2009). Figure 1.6 shows the trail system for orangutan behavioural research in Suaq Balimbing.

Figure 1.7 – Ketambe Trail System



Ketambe

The Ketambe research site (Figure 1.4) was established in 1971 for research on the Sumatran orangutan (*P. abelii*). It is situated at an altitude of approximately 350 m above sea level, with elevations to 450 m (Rijksen, 1978). It lies in the northeast of the Gunung Leuser Ecosystem (3° 41′ N, 97° 39′ E) and experiences two wetter and two drier periods with a mean annual rainfall of 3,288 mm (Wich and van Schaik, 2000). Ketambe is composed of a series of Holocene alluvial terraces in the upper parts of the Alas River valley, and on the lower slopes of the adjacent mountain ranges of Gunung Mamas, to the west, Gunung Kemiri, to the north and Gunung Bandahara to the east (Rijksen, 1978; van Schaik and Miranto, 1985). The study area is bordered by the Ketambe River and the Alas River (Figure 1.7).

The forest at Ketambe is mainly composed of primary mixed dry lowland forest, with some alluvial forests along the Alas and Ketambe rivers (Rijksen, 1978; van Schaik and Miranto, 1985), rather than dipterocarp forest as trees of the family Dipterocarpaceae are not particularly common, accounting for only 4% of trees (Whitten et al., 2000). Instead, Ketambe is characterised by an abundance of trees from Meliaceae and Moraceae, which produce fleshy, animal dispersed fruits (Palombit, 1992). Ketambe is notable in its high density of strangling figs (*Ficus* spp.) which are responsible for the occurrence of orangutan feeding aggregations at this site (Sugardjito et al., 1987). Densities of orangutans in Ketambe are estimated to be 3.24 ind/km^2 (based on standardised density estimates, Husson et al., 2009).

1.7 Aims and Objectives

The main objective of this thesis is to expand our understanding of orangutan locomotion and how this relates to both forest structure and species differences between Borneo and Sumatra. Whilst orangutan locomotor behavior in mixed dry forest in Sumatra has been well studied, their locomotor behavior in peat-swamps is poorly understood. Thus, the primary aim of this study is to add to our current knowledge, by examining the locomotor behavior of orangutans in two peat-swamp forest sites, one in Central Kalimantan, Borneo (Sabangau) and one in the Leuser Ecosystem, Aceh Province, Sumatra (Suaq Balimbing). This data is compared with observations from mixed dry forest also in the Leuser Ecosystem, Aceh Province, Sumatra (Ketambe, Thorpe and Crompton, 2005, 2006, 2009). An in-depth assessment of forest structure and support availability was undertaken at all three orangutan study-sites in order to advance our

understanding of how this large arboreal ape interacts with such a complex and dynamic environment. Little is known about whether orangutan species differ post-cranially (Thorpe and Crompton, 2009). A further aspect of this study employs a non-invasive technique to measure the limb lengths of wild orangutans in Borneo and Sumatra to ascertain if there are any differences in the limb proportions between the two species. In addition, measurements were obtained from an orangutan rehabilitation centre in Borneo, which will allow the assessment of limb proportions between the age-sex clasess and increase our knowledge of the postcranial anatomy of this great ape.

1.8 Thesis Overview

This thesis is organised into eight chapters, **chapters 2 – 7** are written as separate papers, three of which have already been submitted to peer reviewed journals, however, as a result there is a degree of overlap, particularly in the method sections. Since previous studies of orangutan locomotor behaviour have been concentrated in dry lowland forest, we wanted to add to current knowledge by investigating orangutan locomotion in a different species and a completely different forest type. **Chapters 2** and **3** focus on the locomotor behaviour of orangutans in disturbed peat-swamp forest in Sabangau, Central Kalimantan, Borneo on the subspecies *Pongo pygmaeus wurmbii*. In **Chapter 2**, we examine the locomotor behavior of wild orangutans in relation to height in the canopy, age-sex class, behavior (feeding or travelling), and the number of supports used for weight-bearing. **Chapter 3** expands on this by examining how orangutans at the same site interact with their environment in terms of the number, size and type of arboreal supports used during locomotion. Since the quantification of

habitat is an important component in understanding locomotor behavior in an arboreal environment, in **Chapter 4**, we compare forest structure and support availability in all three orangutan study sites. In this chapter we also investigate support preference/avoidance strategies with regard to support use during locomotion. Finally, we explore the characteristics of trees used for travel in the two peat-swamp forest sites. Given known cranio-dental differences between the species, we wanted to try and ascertain if there were also any differences in limb length, so in **Chapter 5**, we present data on the measurement of limb lengths in orangutans using the parallel laser technique. The data collected using this method is compared for the Sumatran species (*Pongo abelii*) and the Bornean sub-species *Pongo pygmaeus wurmbii*. we also present measurements obtained in a rehabilitation centre in Borneo (Nyaro Menteng) on the Bornean sub-species, *P. p. wurmbii*, to add to the current, yet sparse, literature on orangutan post-cranial morphology and how this differs between age-sex classes. In **Chapter 6**, we compared the locomotor behavior across all three study sites to investigate whether the greatest differences in terms of support use were at the habitat or species level, or indeed differed between the three study sites. To fully understand the effect of habitat type on orangutan locomotor behavior we then, in **Chapter 7**, examine whether orangutans in peat-swamp employ the same strategies to control support flexibility as were found in dry forest, or if they have lower thresholds as a result of a more stunted forest structure. Finally, in **Chapter 8**, we bring together the results of this study and discuss the aspects of morphology and habitat on orangutan positional behaviour, and discuss the implications of these results for future studies.

CHAPTER 2

Locomotor Behaviour of Wild Orangutans (*Pongo pygmaeus wurmbii*) in Disturbed Peat-Swamp Forest, Sabangau, Central Kalimantan, Indonesia

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KLM collected and analysed the data and wrote the manuscript, HCM contributed the the writing of the manuscript, SKST developed the methods and contributed to the writing of the manuscript

ABSTRACT

This study examined the locomotor behaviour of wild Bornean orangutans (*P. p. wurmbii*) in an area of disturbed peat-swamp forest (Sabangau Catchment, Indonesia) in relation to height in the canopy, age-sex class, behaviour (feeding or travelling), and the number of supports used to bear body mass. Backward elimination log-linear modelling was employed to expose the main influences on orangutan locomotion. Our results show that the most important distinctions with regard to locomotion were between suspensory and compressive, or, orthograde (trunk vertical) and pronograde (horizontal trunk) behaviour. Whether orangutans were travelling or feeding had the most important influence on locomotion whereby compressive locomotion had a strong association with feeding, suspensory locomotion had a strong association with travel in the peripheral strata using multiple supports, whereas vertical climb/descent and oscillation showed a strong association with travel on single supports in the core stratum. In contrast to theoretical predictions on positional behaviour and body size, age-sex category had a limited influence on locomotion, concurring with previous studies in dry lowland forest. But, orangutans in the Sabangau exhibited substantially higher frequencies of oscillatory locomotion than observed at other sites, suggesting that this behaviour confers particular benefits for traversing the highly compliant arboreal environment typical of disturbed peat-swamp forest. In addition, torso-pronograde suspensory locomotion was observed at much lower levels than in the Sumatran species. Together these results highlight the necessity for further studies of differences between species, which control for habitat.

2.1 Introduction

STUDIES of the positional behaviour exhibited by animals in the wild provide a critical link between their ecology, behaviour, and morphology (Stafford et al., 2003). For primates, Hunt et al. (1996)'s standardisation of the classification of positional behaviour has facilitated far greater precision in inter-specific comparisons of primate locomotor ecology, which promises to greatly enhance our understanding of the evolution of primate locomotor diversity. In this context, the locomotor ecology of orangutans is particularly interesting because they are the largest arboreal primate (Cant, 1987b; Thorpe and Crompton, 2006) and possess post-cranial traits that are particularly adapted for the complex and dynamic arboreal environment in which they live, such as long forelimbs with hook-like hands, short hind-limbs with hand-like feet, and highly flexible hip and shoulder joints (Fleagle, 1999; McLatchy, 1996; Delgado and van Schaik, 2000). While a number of studies of orangutan positional behaviour have been carried out (e.g. Sugardjito, 1982; Sugardjito and van Hooff, 1986; Cant, 1987a) the only comprehensive study of orangutan locomotion, which includes all age-sex categories and a full range of behavioural contexts, studies Sumatran orangutans (*Pongo abelii*) in mixed dry forest (Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007a, b, 2009). Their study suggested that while orangutans exhibit a large repertoire of locomotor behaviour, it is predominantly characterised by orthograde suspensory locomotion, whereby the body is orthograde with the head superior, and various combinations of all four appendages are used to grasp supports in different ways, with suspension by the forelimbs from above (Cant, 1987a; Thorpe and Crompton, 2005).

Orangutans inhabit a wide range of habitats in primary and secondary forest including lowland dipterocarp, freshwater, and peat-swamp forests (Rodman and Mitani, 1987; Knott, 1999; Morrogh-Bernard et al., 2003). Peat-swamp forests support the highest densities of orangutans when compared to other forest types (Husson et al., 2009). Indeed peat-swamp forest provides a home for possibly a third or more of the total Bornean orangutan population and is thus a particularly important orangutan habitat (Meijarrd, 1997; Singleton et al., 2004). While peat-swamp forest covers substantial areas of Kalimantan with ~6.8 mha on its coastal lowlands (Rieley et al., 1996), it supports both a lower density and diversity of species than dry forest (Whitmore, 1984; Prentice and Parish, 1990; Page et al., 1997; Shepherd et al., 1997; Struebig et al., 2007; Harrison et al., 2010). In addition, there are gross differences in forest structure and productivity between Borneo and Sumatra as a result of the younger, more fertile volcanic soils of Sumatran dry forests compared to the more stunted, ombrogenous peat-swamp forest, where all nutrients are received from aerial precipitation (Page et al., 1999; Rijksen and Meijaard, 1999; Marshall et al., 2009; Thorpe and Crompton, 2009; Harrison et al., 2010). These variations in habitat structure and forest productivity are likely to result in substantial differences in positional behaviour between orangutan species; indeed many of the morphological, social, and cultural differences recently documented between Bornean and Sumatran orangutans have been attributed to these differences in forest quality (Taylor and van Schaik, 2007; Marshall et al., 2009; van Schaik et al., 2009).

Undisturbed lowland peat-swamps generally have a medium (35-40 m) to low (15-25 m) forest canopy, with mixed swamp forest having a closed

canopy layer between 15 and 25m (Page et al., 1999). In contrast, mixed dipterocarp forests are much taller with the top of the canopy being typically 45 m (Whitmore, 1984). A typical peat-swamp forest has a very different structure to dryland forest with larger canopy gaps and a thicker understorey compared to a more continuous upper canopy with a sparse understorey typified by dryland forest. Selective logging can further bring about large gaps between emergent trees, while increasing the quantity of vegetation in the lower canopy, which also results in a more rugose and discontinuous forest canopy (Vogel et al., 2009). Together these factors might be expected to cause orangutans in peat-swamp forest, and particularly disturbed peat-swamp forest, to travel at lower heights than in dipterocarp forest or to resort to terrestrial travel, which would greatly increase the cost of locomotion (Thorpe et al., 2007a). Alternatively however, the flexibility (compliance) of supports at this level may instead facilitate travel through tree-sway (where orangutans oscillate compliant supports with increasing magnitude to cross gaps). Oscillation has been shown to reduce the energetic cost of gap crossing when compared to jumping or descending to the ground and crossing terrestrially (Thorpe et al., 2007a). Coupled with this, the high density of smaller trees in disturbed forest will reduce the availability of larger, stable supports and orangutans may therefore need to compensate by utilising multiple supports to support their body mass more often than orangutans in dipterocarp forest which is characterised by large emergent trees.

Orangutans show extreme sexual dimorphism; adult male orangutans weighing between 80 and 91 kg, more than twice that of adult females (33-45 kg) (figures are from Markham and Groves, 1990 for Bornean

orangutans) and un-flanged males. The latter are about the same size as adult females but lack the secondary sexual characteristics possessed by flanged males (Galdikas, 1985; Kingsley, 1988). While data currently available on the post-cranial anatomy of orangutans is limited, Bornean and Sumatran orangutans are generally considered to be of broadly similar size (Smith and Jungers, 1997). Theoretical predictions of the relationship between positional behaviour and body mass (Cartmill and Milton, 1977), which imply that larger animals should suspend more than smaller ones, have not been borne out by the study of Sumatran orangutans (Cant, 1987a; Thorpe and Crompton, 2005). However, whereas in Sumatra orangutans rarely descend to the ground due to the presence of the Sumatran tiger (*Panthera tigris sumatrae*), (Sugardjito and van Hooff, 1986), in Borneo flanged males are known to spend a significant proportion of their time travelling on the ground (MacKinnon, 1974; Galdikas, 1978; Rodman, 1979a; Tuttle, 1987), and sub-adult males and adolescent females have also been observed occasionally to travel substantial distances over the ground (Manduell, personal observations). How body size affects arboreal travel in a depauperate peat-swamp forest is interesting as the prevalence of small trees, reduced availability of larger supports for travel, and possibly higher incidence of canopy gaps compared to pristine dipterocarp forest is likely to pose a greater challenge for such large bodied arboreal primates, suggesting that there may be a greater association between body size and locomotion than has been observed in Sumatra (Cant, 1987a; Thorpe and Crompton, 2005). To date the only study on the positional behaviour of Bornean orangutans focused on two adult (*P. p. morio*) females (Cant, 1987b), thus precluding the assessment of the association between suspension and body mass. This is therefore the first comprehensive study of Bornean orangutans

which includes all age-sex categories.

Given the importance of peat-swamp forests as wild orangutan habitats, this study aims to build on previous work through a comprehensive study of the locomotor behaviour of a population of wild Bornean orangutans (*P. p. wurmbii*) in an area of disturbed peat-swamp forest. In this study we attempt to identify the most important interactions between Bornean orangutan locomotion and age-sex class, height in the canopy, behaviour and the number of supports used for weight bearing to see if the same associations apply as were found for Sumatran orangutans (*P. abelii*) in pristine dry lowland forest. Specifically, we hypothesize that there will be 1) an increased frequency of tree-sway given the high density of small compliant trees; 2) an increased frequency of multiple support use in order to compensate for the lack of larger stable supports; 3) a stronger association between age-sex class and locomotion given the lack of larger stable supports and opportunities for terrestrial travel; 4) an increased frequency of suspensory locomotion to increase stability, and 5) a tendency for orangutans to travel at lower levels, given the more depauperate forest structure.

2.2 Methods

Field Study

The field study took place between March and September 2007, and April 2009 and January 2010. Field research was carried out as part of the OUTROP-CIMTROP multi-disciplinary research project within the LAHG (Laboratorium Alam Hutan Gambut: Natural Laboratory for the Study of

Peat Swamp Forest), a 500 km^2 area of forest located at the northern end (02°19'S; 113°54'E) of the Sabangau forest, Central Kalimantan, Indonesia. The Sabangau catchment ranges from pristine to disturbed peat-swamp forest and comprises 6,000 km^2 of 22,000 $km^2$of tropical peat-swamp found in this region. The area was described in detail by Page et al. (1999), but see also Morrogh-Bernard (2003)and Buckley et al. (2006). Orangutans in the NLPSF have been studied continuously since 2003, thus are known and habituated to observers.

The study site was a logging concession from 1966 to 1996 and almost as soon as the logging concession expired, illegal logging started, which was eventually stopped in the immediate study area in 2004. However, many gaps in the forest canopy remain as a result of sustained disturbance, not only through the direct removal of trees but also through the creation of canals and skids in order to transport logs out of the forest. Canals have an important impact on forest structure, as peat drainage leads to increased incidence of tree falls (Watson et al., 2000; D'Arcy and Page, 2002). Bat hunting was also prevalent in the study area which creates clearings in order to trap bats (Struebig et al., 2007). Together these factors have resulted in a forest structure which has a very thick understorey with large gaps between trees in the upper canopy.

The study was conducted in a 4 km^2 area of disturbed peat-swamp forest and all observations were made by a single observer (KLM) to ensure consistency. Once an orangutan was located it was followed until it made its night nest (15:00h - 19:00h). The nest was returned to on the following morning, before dawn (04:30h). Once the animal arose from its nest it was

then followed from nest-to-nest for a period of up to 10 days within a 30-day period, or until it went out of the research area. Detailed observations of locomotion, height in the canopy, behaviour and the number of supports used to bear body mass were collected using focal instantaneous sampling on the 1-min mark, using a digital watch with a countdown-return vibration alarm function. Details of data collected at each sample point are presented in Table 2.1. Self-training in the estimation of positional modes and heights was undertaken prior to the collection of data and repeated training in estimating height was carried out throughout the data collection period in order to ensure accuracy. The classification of positional behaviour follows that detailed by Hunt et al. (1996) but also includes additional positional modes described by Thorpe and Crompton (2006). While 47 biomechanically distinct locomotor submodes were identified during the course of the data collection period, for the purposes of the present study they are conflated into the seven submodes detailed in Table 2.1 (after Thorpe and Crompton, 2005).

Twenty-two individuals were observed, including all age-sex categories. Adult or flanged males were defined as those exhibiting secondary sexual characteristics such as cheek flanges, throat pouches, and increased body mass, adult females were those females that had given birth or were old enough to have had offspring whether in parturition or not. Sub-adult or unflanged males were those which were sexually active but lacked secondary sexual characteristics, and immature females were those showing no sexual activity (Rijksen, 1978). Thirty-six percent of all observed locomotor bouts sampled the behaviour of adolescent males and females (four individuals), 30% sampled adult males (eight individuals), 17%

Table 2.1 – Positional Behaviour Observations[a]

1. **Date**
2. **Individual**
3. **Time**
4. **Positional mode**[b]
   1. Quadrupedal Walk: Locomotion on top of supports angled at <45° of true horizontal; typically all four limbs contact the support in a particular sequence. The torso is pronograde (–) or roughly parallel to the support. Includes tripedal walk, quadrupedal run, and tripedal run.
   2. Bipedal Walk: Hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. Includes flexed and extended bipedalism, and hand-assisted bipedalism in which hindlimbs bear more than 50% of body mass, but one or both forelimbs are used to assist, either in suspension or compression, and bear more than their own weight.
   3. Climb/descent[c]***:*** Ascent and descent on supports angled at ≥45°. Distinction is made between vertical climb/descent (within 20° of true vertical) and angled climb (between 20° and 45° of true vertical).
   4. Torso-orthograde suspension[c]***:*** Includes brachiation and orthograde clamber which is a forelimb suspensory torso-orthograde mode (|), but with hindlimbs assisting. All the four limbs act as propulsors, with most body weight borne by the abducted forelimbs. Also includes the mode drop, in which all pre-drop postures were orthograde in nature.
   5. Torso-pronograde suspension[d]***:*** All the four limbs are used in some combination; the torso is pronograde, and limbs are in tension.
   6. Bridge[d]***:*** A torso-pronograde gap-closing movement where the hands reach out to grasp a support on one side of a gap and cautiously pull the body across the open space with the feet retaining their grips until a secure position is established on the other side . A gap is therefore defined for this purpose as where there is open space between the peripheral branches of neighbouring trees.
   7. Oscillation: Combines modes tree sway and ride. Tree sway is a gap crossing movement used between trees where either body weight or oscillation are used to deform branches, and often the pre-gap closing posture resembles clinging more than suspension. Ride is similar to tree sway, but is used from tree to ground, although it can also be used to move from a higher to a lower level in the canopy as in Thorpe and Crompton (2005). A small diameter support is grasped in a clinging posture and a movement or oscillation overbalances the support. The weight of the individual's body pulls the support from a vertical orientation toward horizontal. As the support approaches horizontal a suspensory posture may result, after or during which the grip with the hindlimb is released and the feet contact the ground/support(s) at a lower level in the canopy.
5. **Height:** 5m intervals up to 30m, >30m (measured as the vertical distance from the animal to the ground).
6. **Number of Supports:** 1, 2, 3, 4, >4.
7. **Support Type:** Branch, bough, trunk, liana, other (aerial roots, nest).
8. **Support Diameter:** <2cm; ≥2 - <4cm; ≥4 - <10cm; ≥10 - <20cm; ≥20 - <40cm; ≥40cm.
9. **Behaviour:** Feeding (acquiring, processing, and eating); travelling.

[a] Data collection followed Thorpe and Crompton (2005)

[b] All follow those of Thorpe and Crompton (2006), which were based on Hunt et al. (1996).

[c] For analysis, angled climb/descent was included with torso-orthograde suspensory locomotion following Thorpe and Crompton (2005).

[d] For analysis, pronograde suspension and bridge were conflated, as both had very small frequencies and are functionally similar.

sub-adult males (five individuals), and 17% adult females (five individuals), (see Appendix A).

Statistical Analysis

The interdependence of observations is a particular problem in the analysis of positional behaviour as sequential observations using a small time interval are thought to be highly dependent, thus complicating statistical analysis (Mendel, 1976; Janson, 1984; Hunt, 1992, 1994; Dagosto, 1994; McGraw, 1996; Warren and Crompton, 1997; Cant et al., 2001; Thorpe and Crompton, 2005). While some studies have chosen to omit statistical tests of significance, instead only presenting frequencies (e.g. Cant, 1987a), others have employed a variety of procedures in order to deal with the violation of independence (e.g. Janson, 1984; Hunt, 1992; Dagosto, 1994; Gebo and Chapman, 1995; McGraw, 1996; Cant et al., 2001). However, when observing orangutan locomotion in the wild, sequential observations (i.e. observations taken on consecutive minute samples) of locomotion are relatively uncommon because visibility is severely impeded by dense foliage and orangutans also tend to rest frequently during travel bouts (Thorpe and Crompton, 2005, personal observations). Furthermore, the low canopy and small trees that characterise the Sabangau means that even in longer bouts of locomotion, orangutans must change locomotor behaviour frequently as they navigate a rapidly changing locomotor environment. In this study, while sequential observations of locomotor behaviour accounted for 26% of the total number of observations, only 6.7% of this total were sequential observations where the same locomotor mode or submode was observed. Given the high density of small trees which are commonly used by

orangutans during travel in the Sabangau forest, even those 6.7% are not necessarily the same locomotor bout and orangutans are likely to have changed trees and used different locomotor modes or paused briefly between minute samples. It was therefore felt that the dependence between data points was negligible and all locomotor observations obtained in this study were analysed (after Thorpe and Crompton, 2005).

Categorical data of the sort collected in this study are typically summarised in contingency tables and tested by chi-square or log likelihood (G-test) procedures (Cant et al., 2001). However, while valid for two-dimensional analyses, analysis of multidimensional contingency tables using a series of all possible combinations of two-dimensional tables is not an appropriate technique as it may lead to misleading conclusions being drawn (Gilbert, 1981; Agresti, 1990). Consequently, backward elimination log-linear models were used to analyse multiple relationships between the variables collected in this study using SPSS version 15.0.

Backward elimination log-linear modelling was used to analyse multiple relationships between locomotion, age-sex category, behaviour, height in the canopy and support use using SPSS version 15.0. Log-linear analysis is a technique for analysing categorical or frequency data. Note that a significant value of 1 for the χ^2 likelihood ratio indicates a perfect fit of the model's predicted cell counts to the observed cell counts, although a P value of >0.05 is considered significant (Thorpe and Crompton, 2005; Thorpe et al., 2007b).

The variable interactions (i.e. model expressions) produced by log-linear models can be analysed in more detail in order to investigate the nature of

Table 2.2 – Substitute classifications tested in log-linear analysis

Original variable	Substitute classification	Categories
1. Age-sex	Sex	1) male, 2) female
	Age 1	1) adult male + adult female + subadult male, 2) adolescent
	Age 2	1) adult female + adult male, 2) subadult male + adolescent
	Age-sex 1	1) adult female, 2) adult male; subadult male, 3) adolescent
	Age-sex 2	1) adult female, 2) adult male + subadult male, 3) adolescent
	Age-sex 3	1) adult female + subadult male, 2) adult male, 3) adolescent
	Age-sex 4	1) adult male, 2) adult female + subadult male + adolescent
2. No. of supports[1]	No. of supports 1	1; 2; 3; 4; >4
	No. of supports 2	1; 2-4; >4
	No. of supports 3	1; >1
3. Height	Height 1	1) <10 m, 2) 10-15 m, 3) >15 m
	Height 2	1) <10 m, 2) >10 m
	Height 3	1) <15 m, 2) >15 m
	Height 4	1) 5-15 m (core stratum), 2) <5 m + >15m (peripheral strata)
4. Locomotion	LOCO-a	1) quadrupedal, 2) bipedal, 3) orthograde suspend, 4) pronograde suspend, 5) climb/descent, 6) oscillation
	LOCO-b	1) quadrupedal, 2) orthograde suspend + bipedal walk, 3) pronograde suspend, 4) climb/descent, 5) oscillation
	LOCO-c	1) quadrupedal + pronograde suspend, 2) bipedal + orthograde suspend, 3) climb/descent, 4) oscillation
	LOCO-d	1) quadrupedal + bipedal, 2) orthograde suspend + pronograde suspend, 3) climb/descent, 4) oscillation
	LOCO-e	1) quadrupedal + bipedal, 2) orthograde suspend + pronograde suspend, 3) climb/descent + oscillation
	LOCO-f	1) quadrupedal + pronograde suspend, 2) bipedal + orthograde suspend, 3) climb/descent + oscillation
	LOCO-g	1) quadrupedal + pronograde suspend, 2) orthograde suspend, 3) bipedal + climb/descent, 4) oscillation
	LOCO-h	1) suspension, 2) compression, 3) mix (submodes incorporating both compression and suspension within a bout e.g tree sway)
	LOCO-i	1) pronograde, 2) orthograde, 3) oscillation

[1] Semi-colons partition variables into different categories.

Table 2.3 – The Five Statistically Best Fitting Models

Model[1]	Chi-square	DF	P value	Model Expressions (variable relationships)[2]	Partial χ^2	DF[3]	Standardised χ^2 (χ^2/DF)[4]
Age1*Behaviour*Supports3*Height4*LOCOe	2.407	8	0.966	locomotion*behaviour*no. of supports	156.878	2	78.439
				behaviour*height*locomotion	17.973	2	8.99
				age*behaviour*locomotion	12.04	2	6.02
				age*no.of supports*height*locomotion	7.54	2	3.77
				age*behaviour*no.of supports*height	3.298	1	3.298
Age2*Behaviour*Supports3*Height4*LOCOe	6.673	14	0.947	behaviour*no. of supports*locomotion	153.375	2	76.688
				behaviour*height*locomotion	18.425	2	9.2125
				behaviour*age-sex*locomotion	15.953	2	7.9765
				no. of supports*height*locomotion	11.64	2	5.82
				behaviour*no. of supports*age-sex*height	3.505	1	3.505
Age1*Behaviour*Supports3*Height4*LOCOf	3.446	8	0.903	behaviour*no.of supports*locomotion	138.97	2	69.485
				behaviour*height*locomotion	14.15	2	7.075
				age*behaviour*locomotion	9.76	2	4.88
				age*no.of supports*height*locomotion	9.292	2	4.646
				age*behaviour*no.of supports*height	3.666	1	3.666
Sex*Behaviour*Supports3*Height3*LOCOf	10.5	16	0.839	behaviour*sex*height	9.27	1	9.27
				behaviour*no.of supports*locomotion*height	12.766	2	6.383
				locomotion*sex*height	9.699	2	4.8495
Sex*Behaviour*Supports3*Height1*LOCOf	10.062	15	0.816	supports*height*behaviour*locomotion	24.942	4	6.2355
				supports*height*locomotion*sex	8.047	4	2.012
				behaviour*height*sex	14.107	2	7.0535

[1] For details of variable categories in each model refer to (Table 2.2). For example, Age1 separates 1) adult males + adult females + subadult males and 2) adolescents.
[2] Asterisks delineate variables included in the model expressions.
[3] DF, degrees of freedom.
[4] Large standardised χ^2 values correspond to the most important interactions and are ranked for each model accordingly.

associations between variables through contingency tables containing row and column percentages and standardised cell residuals (SCRs). Standardised cell residuals indicate by their sign whether an interaction is more (positive values) or less (negative values) common than predicted by the model and, by their size, to what degree. Standardised cell residuals greater than ±2 indicate a substantial variation from the model predictions and, therefore may be of particular interest (Thorpe and Crompton, 2005; Thorpe et al., 2007b). Odds ratios also aid interpretation of the patterns in the data. These represent ratios of probabilities and are used to establish correlations which underlie significant associations (Crook, 1997). For example, for the interaction height * locomotion, of the 1,407 observations of "torso orthograde suspension", 1264 took place below 15m with 143 above 15m. Therefore, the probability that "torso orthograde suspension" will take place below 15m is 1264/1407 = 0.9, and the probability that it will take place above 15m is 143/1407 = 0.1. The odds ratio of these probabilities is 9 (0.9/0.1) which establishes a correlation between height and "torso orthograde suspension" which is 9 times more likely to take place below 15m than above.

The power of log-linear analysis is weakened if more than 20% of cells within a multiway contingency table have an expected value of less than 5 (Tabachnick and Fidell, 1996) or if any sampling zeros exist. Consequently, it was necessary to conflate variables in order to meet these criteria. In order to ascertain the most suitable substitute variables, categories were reclassified in alternative ways (Table 2.2) and all possible combinations were tested. The manner in which variables were classified followed (Thorpe and Crompton, 2005), with locomotor modes being combined on a

basis of broad biomechanical similarities. For example, in some variable classifications, bipedalism and orthograde suspension were combined as the body is held in an orthograde position (e.g. LOCO-c, LOCO-f) whereas in others bipedalism was combined with quadrupedalism as both utilise compressive body positions (e.g. LOCO-d, LOCO-e).

Models for all combinations of variables were assayed and then ranked in order of P-value. The five statistically best-fitting models are detailed in Table 2.3. The model "age-2 * behaviour * no. of supports * height4 * LOCO-e" (P = 0.947, Table 2.3) was selected as it had the second highest P-value but resolved one of the complex first order interactions into a simpler, second order, interaction. The variable interactions retained in this model, following the backward elimination log-linear analysis, are therefore discussed in more detail. However, it is notable that LOCO-f also produced well fitting models and are also discussed in further detail.

2.3 Results

Descriptive Data

A total of 18,220 instantaneous observations of positional behaviour were obtained; 15,346 of postural behaviour and 2,874 of locomotion. Only the latter are presented in the current paper. Orthograde suspensory locomotion dominated orangutan locomotion accounting for 47.9% of observations. Orangutans are 2.5 times more likely to exhibit orthograde suspension than oscillation and 3.3 times more likely than vertical climb/descent. Orangutans exhibited orthograde suspension 5.6, 11.6, and 15.3 times more often than quadrupedalism, pronograde suspension, and bipedalism,

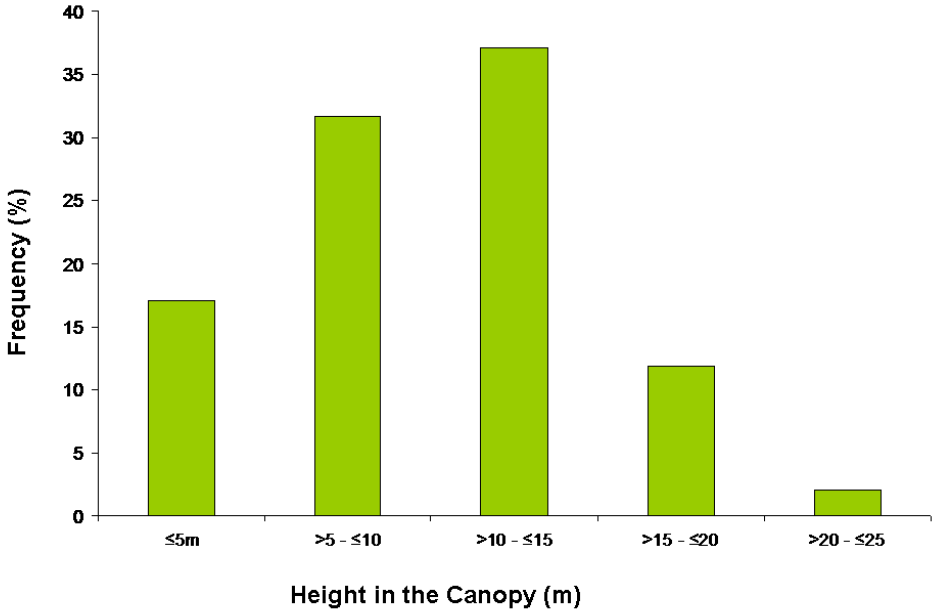
respectively (Table 2.4). Eighty-four percent of all observed locomotor bouts were exhibited during travel with 16% during feeding. Sixty-nine percent of all observations of locomotion took place in the core stratum (>5m - ≤15m) and 63.9% took place on multiple supports (Figure 2.1, Figure 2.2, respectively).

Table 2.4 – Percentages of Commonly Observed Locomotor Modes According to Behaviour

	Percent (%)		
Mode	**Travel**	**Feed**	**Total**
Quadrupedal and tripedal walk	7.8	12.7	8.5
Walk	*3.8*	*6.3*	*4.2*
Pronograde scramble	*3.8*	*6.3*	*4.3*
Torso-orthograde suspension	50.8	31.7	47.9
Brachiation and forelimb swing	*10.0*	*33.1*	*11.4*
Orthograde clamber and transfer	*46.4*	*10.5*	*40.9*
Torso-pronograde suspension	1.2	1.4	1.3
Forelimb/hindlimb swing	1.0	1.1	1.0
Bipedal walk	2.6	6.8	3.2
Bipedal walk	*0.1*	*0.0*	*0.1*
Assisted bipedal walk	*2.4*	*6.8*	*3.1*
Bridge	2.0	2.0	1.9
Vertical climb	7.6	22.7	10.0
Vertical descent	4.1	10.7	5.1
Drop	1.0	1.1	1.0
Sway	20.8	9.1	19.0
Ride	0.8	0.7	0.8

Quadrupedal and tripedal walk accounted for 8.5% of all locomotor behaviour and accounted for 7.8% of all locomotion during travel and 12.7% of all locomotion during feeding. The submode *Walk* ccounts for 6.3% of all locomotion during feeding and 3.8% of all locomotion during travel.

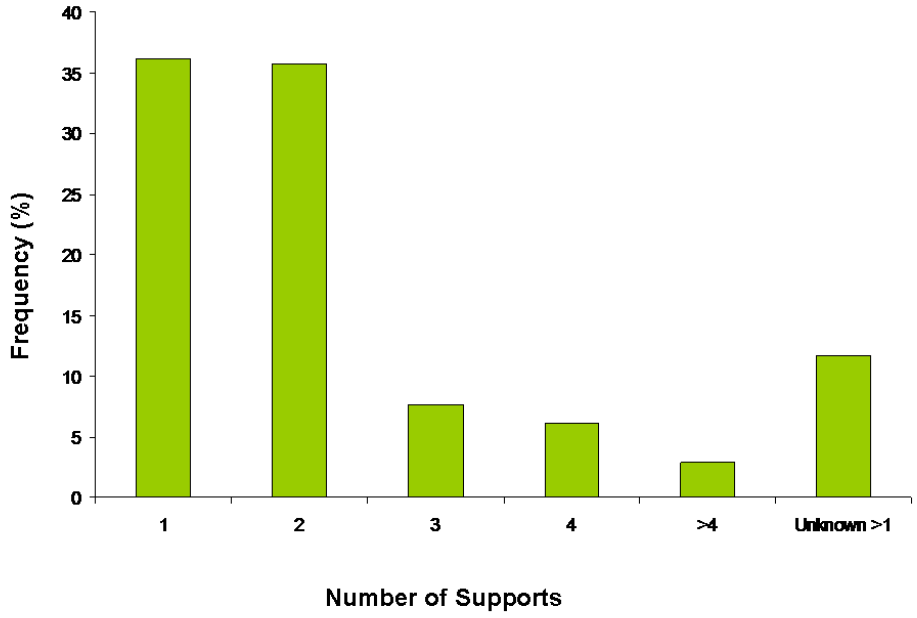
Figure 2.1 – Frequency of Heights Used During Locomotion



Variable Associations

All of the variables included in the models were classified in alternative ways in order to expose the main influences on orangutan locomotion. Height was reclassified in a number of different ways Table 2.2, but when described in terms of core stratum (>5m - ≤15m) and peripheral strata (≤5m; >15m) it was more effective in explaining the relationship between all of the variables by consistently producing better fitting models (defined as the balance between a high P value but simple model expressions). Similarly, better fitting models were produced when the number of supports differentiated between the use of single and multiple supports. Locomotion was best explained when it was differentiated into suspensory postures whereby the body is presumptively under a predominantly tensile stress

Figure 2.2 – Frequency of Number of Supports Used During Locomotion



regime suspended beneath supports (orthograde suspension + pronograde suspension) and compressive postures whereby the body is in compression, above supports (quadrupedalism + bipedalism), and when climb and descent was combined with oscillatory locomotion, which although are functionally different, both are predominantly orthograde. Age-sex class produced better fitting models when expressed in terms of age alone; when it was differentiated into smaller categories, to reflect both age and sex class, the resultant models had lower P-values.

The final model of best fit that was selected for analysis is presented in Table 2.5, with the associated standardised χ^2 values revealing the expressions that contributed most to the significance of the model. The

Table 2.5 – The Statistically Best Fitting Model

Model[a]	χ^2	**DF**	**P-value**
age * behaviour * height * locomotion * no. of supports	6.673	14	0.947
Model expressions (variable relationships)[b]	**Partial χ^2**	**DF**[c]	**Standardised χ^2 (χ^2/DF)**[d]
behaviour * no. of supports * locomotion	153.375	2	76.688
behaviour * height * locomotion	18.425	2	9.213
behaviour * age * locomotion	15.953	2	7.977
no. of supports * height * locomotion	11.640	2	5.820
behaviour * no. of supports * age * height	3.505	1	3.505

[a] Age (adult male + adult female; subadult male + adolescent), Behaviour (feeding; travelling), Supports (1; >1), Height (core stratum 5-15m; peripheral strata <5m, >15m); Locomotion (compression; suspension; climb/descent + oscillation).

[b] Asterisks delineate variables included in the model expressions.

[c] DF, degrees of freedom

[d] Large standardised χ^2 values correspond to the most important interactions and are ranked for each model accordingly.

variable relationships from the backward elimination log-linear analysis reveal that all the variables included in the final model influenced locomotion to some extent, with the exception of sex class (Table 2.5). In the three most important model expressions, behaviour and locomotion were conditionally dependent given the number of supports used (no. of supports), height and age. Thus, the number of supports used for different types of locomotion differed when feeding or travelling (behaviour * no. of supports * locomotion); locomotion at different heights also varied when feeding or travelling (behaviour * height * locomotion) and the locomotion of adult orangutans to that of sub-adults and adolescents (behaviour * age * locomotion). The number of supports used for different types of locomotion also differed according to whether orangutans were travelling in the core stratum (>5m - $\leq$15m) or in the peripheral strata ($\leq$5m; >15m). However, the standardised χ^2 values show that the combined influence of behaviour and the number of supports accounted for substantially more of the variation in in locomotion than did the combined influence of behaviour and height; behaviour and age or height and number of supports. Finally, the third-order interactions (behaviour * no. of supports * age * height) suggests that the number of supports used by the two age groups when feeding or travelling differs according to height in the canopy, but this relationship was the weakest in the model.

Analysis of Contingency Tables

Table 2.6 provides the contingency table for the model interaction behaviour * no. of supports * locomotion. The high SCRs indicate that quadrupedalism and bipedalism (compression) are positively associated with multiple support use (SCR - 3.4) and negatively associated with single support use

(SCR=-3.1) during feeding but not during travelling. Suspensory modes (i.e., orthograde and pronograde suspension) during travel were also positively associated with multiple support use and negatively associated with single support use (Table 2.6, row percentages), with orangutans being >7 times more likely to use multiple supports than a single support. The modes vertical climb/descent an oscillation were strongly positively associated with single supports use during travel (SCR = 17.6) and negatively associated with multiple support use (SCR = -12.3), but no substantial association existed for feeding.

Table 2.6 – Contingency Table for Model Interaction: locomotion * behaviour * no. of supports[a]

		No. of supports		
Behaviour	**Locomotion[b,c]**	**1**	**>1**	**Total**
Feed	Compression	30.0 (10.0)	70.0 (28.9)	(18.4)
		-3.14	*3.4*	
	Suspension	64.8 (44.4)	35.2 (29.9)	(37.9)
		1.6	*-1.8*	
	Climb/descent + Oscillation	57.9 (45.6)	42.1 (41.2)	(43.7)
		0.5	*-0.5*	
Total		55.4	44.6	100
Travel	Compression	30.4 (8.8)	69.6 (9.8)	(9.5)
		-0.6	*-0.4*	
	Suspension	12.0 (20.8)	88.0 (74.2)	(56.8)
		-13.4	*9.3*	
	Climb/descent + Oscillation	67.9 (70.4)	32.1 (16.1)	(33.8)
		17.6	*-12.3*	
Total		32.6	67.4	100

[a] Entries are row % and (column %) for each behaviour * locomotion * no. of supports unit, e.g., 30% of all compressive locomotion during feeding was on single supports and 10% of all locomotion on singles supports during feeding was compressive locomotion. Standardised cell residuals are in *italics* (negative values indicate frequency is lower than expected).

[b] Compression includes the modes bipedal, tripedal and quadrupedal walk.

[c]Suspension includes the modes torso-orthograde suspension and torso-pronograde suspension.

In contrast, when the relationship between locomotion and behaviour was stratified by height in the canopy (Table 2.7), the values during feeding did

not deviate far from those expected by the model. During travel suspensory behaviours dominated orangutan locomotion in both the core and peripheral strata, but, whereas suspension occurred much more than predicted by the model during travel in the peripheral strata (SCR = 3.8), it occurred much less than predicted in the core stratum. In contrast "vertical climb/descent and oscillation" showed the opposite pattern, being positively associated with travel in the core stratum (SCR = 2.7) and negatively associated with travel in the peripheral strata (SCR = -4.3).

Table 2.7 – Contingency Table for Model Interaction: locomotion * behaviour * height[a]

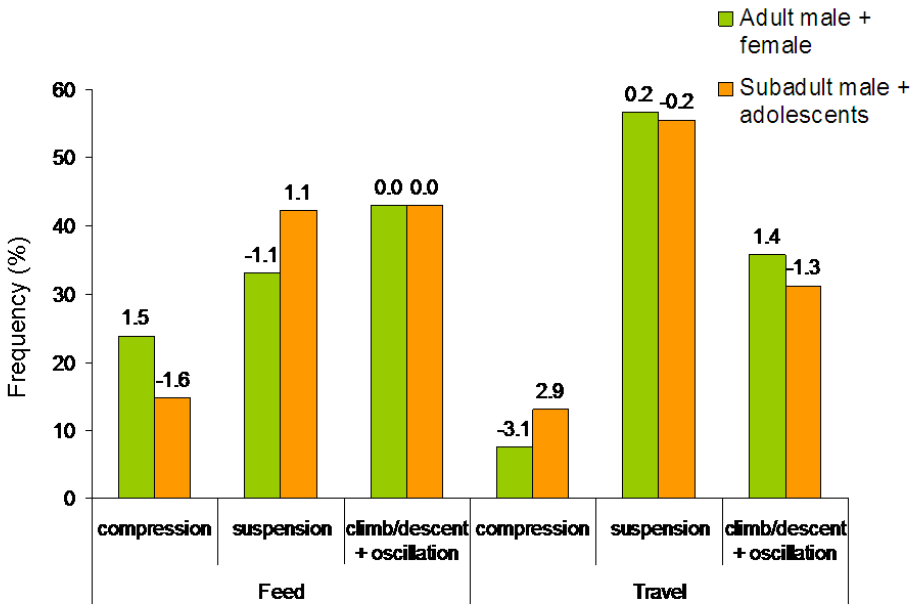
		Height		
Behaviour	**Locomotion**	**Core Stratum**	**Peripheral Strata**	**Total**
Feed	Compression	45.7 (13.9)	54.3 (19.5)	(16.5)
		-1.0	*1.0*	
	Suspension	61.8 (44.3)	38.2 (32.3)	(38.8)
		1.3	*-1.5*	
	Climb/descent + Oscillation	50.5 (41.7)	49.5 (48.2)	(44.7)
		-0.7	*0.7*	
Total		54.1	45.9	100
Travel	Compression	76.4 (9.0)	23.6 (6.9)	(8.4)
		0.8	*-1.3*	
	Suspension	65.9 (53.0)	34.1 (68.6)	(57.5)
		-0.5	*3.8*	
	Climb/descent + Oscillation	79.5 (38.0)	20.5 (24.5)	(34.2)
		2.7	*-4.3*	
Total		71.4	28.6	100

[a] For explanation of table, see Table 2.6

The relationship between locomotion and behaviour also altered when age was taken into account, and while most locomotion did not differ significantly from the expected values (SCRs, Figure 2.3), it is clear that adults tended to avoid (SCR = -3.1) and adolescents and sub-adult males tended to select for quadrupedalism and bipedalism during travel (SCR = 2.9). Compressive locomotion during travel was twice as likely to be seen in

adolescents as adults (see Figure 2.3), whereas the converse was true during feeding, with adults 1.7 times more likely to exhibit compressive locomotion than adolescents.

Figure 2.3 – Model Interaction: Locomotion * Age * Behaviour



** Figures are standardised cell residuals*

When the relationship between locomotion and the number of supports was stratified by height it is clear that suspensory locomotion in both the core stratum and peripheral strata was strongly associated with multiple supports (large positive SCRs, Table 2.8). The relationship between "vertical climb/descent and oscillation" and the number of supports was also similar in the two height strata, with a strong association with single supports and negative association with multiple supports (SCR = 3.4) and a very negative association with multiple supports (SCR = -4.4). However, in the peripheral strata these did not differ substantially from the values expected by the

model.

Table 2.8 – Contingency Table for Model: height * no. of supports * locomotion[a]

		No. of Supports		
Height	**Locomotion**	**1**	**>1**	**Total**
Core Stratum	Compression	16.8 (4.4)	83.2 (12.5)	(9.6)
		-4.4	*3.4*	
	Suspension	18.6 (26.4)	81.4 (66.7)	(52.0)
		-9.4	*7.2*	
	Climb/descent + Oscillation	65.9 (69.2)	34.1 (20.7)	(38.5)
		13.2	*-10*	
Total		36.6	63.4	100
Peripheral Strata	Compression	30.6 (9.2)	69.4 (10.0)	(9.7)
		-0.3	*0.2*	
	Suspension	15.9 (29.7)	84.1 (75.3)	(60.5)
		-6.7	*4.6*	
	Climb/descent + Oscillation	66.5 (61.1)	33.5 (14.7)	(29.8)
		9.7	*-6.7*	
Total		32.4	67.6	100

[a] For explanation of table, see Table 2.6

Table 2.9 provides the contingency table for the four-way interaction age * behaviour * height * no. supports. The partial χ^2 values, which indicate the expressions that contribute most to the significance of the model, were very low for this variable interaction (Table 2.5) indicating that the relationship between these variables is rather weak; indeed the SCR values in the contingency table reveal that the observed values do not differ substantially from the expected values for either feeding or travelling. However, analysis of the odds ratios show that orangutans were 2 and 2.6 times more likely to use multiple supports than single supports in the core and peripheral strata, respectively (Table 2.9, row percentages). During feeding, they used single and multiple supports with similar frequencies (Table 2.9, row percentages).

Table 2.9 – Contingency Table for Model: age * behaviour * height * no. of supports[a]

			No. of Supports		
Behaviour	**Height**	**Age**	**1**	**>1**	**Total**
Feed	Core Stratum	Adult males + females	51.2 (45.6)	48.8 (62.8)	(52.6)
			-1.1	*1.4*	
	Core Stratum	Subadult males + adolescents	67.9 (54.4)	32.1 (37.2)	(47.4)
			1.2	*-1.4*	
Total			59.1	40.9	100
Feed	Peripheral Strata	Adult males + females	47.5 (48.5)	52.5 (53.1)	(50.8)
			-0.3	*0.3*	
	Peripheral Strata	Subadult males + adolescents	52.1 (51.5)	47.9 (46.9)	(49.2)
			0.3	*-0.3*	
Total			49.7	50.3	100
Travel	Core Stratum	Adult males + females	34.9 (47.1)	65.1 (44.4)	(45.3)
			0.6	*-0.5*	
	Core Stratum	Subadult males + adolescents	32.4 (52.9)	67.6 (55.6)	(54.7)
			-0.6	*0.4*	
Total			33.5	66.5	100
Feed	Peripheral Strata	Adult males + females	22.8 (39.8)	77.2 (50.8)	(47.8)
			-1.6	*1*	
	Peripheral Strata	Subadult males + adolescents	31.6 (60.2)	68.4 (49.2)	(52.2)
			1.5	*-0.9*	
Total			27.4	72.6	100

[a] For explanation of table, see Table 2.6

2.4 Discussion

Log-linear modelling allowed for experimentation with different variable classifications. By grouping the data in various ways, it was possible to identify those variable combinations which exposed main data trends with regard to the locomotor behaviour of wild orangutans in the Sabangau forest. The models of best fit combined the locomotor modes vertical climb/descent and oscillation. It is acknowledged that oscillation and climb/descent are functionally different. However, they have a strong association with the use of single and multiple supports, are predominantly orthograde and are associated with travel in the core strata, so more significant models were produced when these two modes were combined.

Locomotion was best understood when modes were combined into compressive postures (quadrupedalism and bipedalism) and suspensory postures (orthograde and pronograde suspension - Table 2.3, Models 1 and 2). However, it is notable that well-fitting models were also produced when locomotor modes were combined into pronograde postures (quadrupedalism and pronograde suspension) and orthograde postures (bipedalism and orthograde suspension - Table 2.3, Models 3, 4 and 5). These results contrast with Thorpe and Crompton (2005)'s study on Sumatran orangutans, where locomotor classifications that incorporated a larger number of categories resulted in higher levels of significance than those which conflated categories into only a few. However, Thorpe and Crompton (2005) note that when locomotor modes were conflated into either suspension and compression or orthograde and pronograde behaviour, they resulted in well-fitting models. Indeed, their most significant model in terms of P-value also combined quadrupedalism with bipedalism (Thorpe and Crompton, 2005; Table 5, p 64), although it retained complex interactions and was therefore rejected in favour of models that combined high P-values with more simple model expressions.

Behaviour was found overall to have the most important influence on orangutan locomotion (as it appeared in the Top 3 expressions of the final model, Table 2.5) suggesting that the locomotion of Bornean orangutans differed substantially when feeding and travelling. However, the influence of behaviour on locomotion varied according to the number of supports used for weight bearing, height in the canopy and age. Quadrupedalism and bipedalism were more commonly associated with feeding than with travelling and were strongly associated with multiple support use during

feeding. This contrasts with the findings of Thorpe and Crompton (2005) where quadrupedalism in Sumatran orangutans was strongly associated with single large supports (>10cm). The Sabangau forest has few horizontal supports of this size and the majority of quadrupedalism observed in this study was irregular gait walking (pronograde scramble) which by definition involves the use of small irregularly placed and variously angled supports (Hunt et al., 1996). It is likely that the lack of suitable supports available for symmetrical gait walking in the canopy is the main reason for the association with multiple support use. In addition, the majority of bipedalism observed was either hand assisted or bipedal scramble and therefore involved the use of multiple supports for weight bearing, as was also found for Sumatran orangutans (Thorpe and Crompton, 2006; Thorpe et al., 2007b)

Our prediction that orangutans in the Sabangau forest are likely to travel lower than observed in dry lowland forest was upheld (Sugardjito and van Hooff, 1986; Thorpe and Crompton, 2005). Orangutans in the Sabangau forest were found to travel predominantly below 20m, with travel above 20m accounting for only 2% of all locomotor observations (**??**), compared with 35% in Thorpe and Crompton (2005). However, in the analysis, height was generally best explained in terms of core stratum and peripheral strata, with 69% of all locomotion taking place in the core stratum between 5 and 15m. This lower canopy provides the most continuous horizontal stratum for orangutan locomotion in the Sabangau forest, particularly given its logging history. Selective logging not only produces large gaps between emergent trees, it also increases the amount of vegetation in the lower canopy. Such rugosity, or irregular canopy structure, results in a

"bottom-heavy" vegetation profile which would therefore increase the number of available structures for support use in the lower strata. Because of the extensive logging that has taken place, the Sabangau forest is likely to be at the extreme end of that gradient. Thus, the upper canopy tends to be virtually one large gap, with a continuous middle canopy now forming the main canopy (Husson, personal communication).

Our prediction that there would be an increased frequency of tree-sway in disturbed peat-swamp forest is also upheld. In fact oscillatory locomotion accounted for 20% of all observations in this study compared with only 7% in both Thorpe and Crompton's (2005) study and Cant's (1987b) study, both of which took place in dry lowland forest. The high density of small, compliant supports in the lower canopy facilitates oscillatory locomotion and is easily exploitable by orangutans. Sugardjito and van Hooff (1986) found higher levels of oscillation for adult males, although this frequency was much lower in Thorpe and Crompton's (2005) study at the same site. This disparity may have been a result of differences in the methods used or the degree of individual variation (Thorpe and Crompton, 2005). In this study, oscillatory locomotion was only slightly higher in adult males (26.4%) than in adult females (22%), and was similarly observed in sub-adult males and adolescents (16.2% and 15%, respectively) indicating that even the younger adolescents are sufficiently heavy enough to oscillate the small trees which dominate this disturbed forest. Thorpe et al. (2007a) found that oscillatory locomotion reduced the energetic cost of locomotion when compared to jumping across a gap or descending to the ground and crossing terrestrially. Since the trees are smaller and thus likely to be more compliant in the Sabangau, the energy cost of tree-sway might be expected to be even

lower than in Sumatra because Bornean orangutans may be able to cross gaps simply by loading the support with their body mass, causing it to deflect in one direction, rather than by active forward and backward oscillations. It is, therefore, possible that orangutans in disturbed forest may be able to exploit the resulting small, compliant trees in order to lower the energetic cost of locomotion.

In terms of the number of supports used during locomotion, our results concur with those of Thorpe and Crompton (2005), as the number of supports used was best understood when multiple supports were combined into a single category. This implies that while both Bornean and Sumatran orangutans use different locomotion on a single support to that on multiple supports, their approach to multiple support use is the same for two supports as for handfuls of foliage (Thorpe and Crompton, 2005). However, our prediction that orangutans in disturbed peat-swamp forest would have an increased frequency of multiple support use in order to compensate for the lack of larger stable supports was not upheld and multiple support use was only slightly higher in this study (63.9%) than observed in dry lowland forest (59%, Thorpe and Crompton, 2005). This similar frequency of single support use is mainly due to the high frequency of tree-sway observed in this study which had a strong association with single support use. The association of oscillatory locomotion with single supports during travel contrasts with the findings of Thorpe and Crompton (2005) where there was a stronger association with multiple tree supports, which allowed orangutans to distribute their body weight onto different supports during tree sway in order to maximise the size of oscillation. This also probably reflects the large number of small trees in the Sabangau forest which can

easily be oscillated about the trunk, rather than requiring the orangutan to move to the periphery of the tree crown, to maximise the moment arm of the sway. Indeed, much of the oscillatory locomotion observed in this study was one-way sway whereby orangutans used their weight to cause the tree to bend laterally (sideways) moving the passenger with it as described by Cant (1987b).

Our prediction that there would be an increased frequency of suspensory locomotion in disturbed peat-swamp forest compared to mixed dipterocarp forest was upheld with 49% of locomotion being suspensory, compared with 39% in mixed dipterocarp forest (Thorpe and Crompton, 2006). However, our predition that there would be a stronger association between age-sex class and locomotion in disturbed peat-swamp forest was not upheld. In the five models of best fit, body size was best explained in terms of age or sex, and in all these, both were found to only have a weak relationship with locomotor behaviour (Table 2.3). Adolescents tended to use compressive postures more during travel than adults, while the converse was true during feeding. Suspensory locomotion increases stability as the individual has in effect already fallen off the support (Thorpe and Crompton, 2009). It is likely that in the Sabangau, the smaller trees used during travel were not sufficiently strong to support adult orangutans in compression. However, in the larger feeding trees the branches probably are sufficiently large enough to support compressive locomotion in adults.

Suspensory locomotion was strongly associated with multiple support use both in the core stratum and peripheral strata. It tended to be positively associated with single supports during feeding, but was very strongly

associated with multiple supports during travel. This is a result of the modes brachiation and forelimb swing being more commonly observed when orangutans travelled within a feeding tree, which typically involved the use of a single support whereas orthograde clamber and transfer were more associated with travel and typically involved multiple supports. In addition, in the core stratum compressive locomotion also showed a positive association with multiple supports. Multiple support use facilitates locomotion on flexible supports and consequently enables orangutans to access the terminal branch niche and minimise path length during travel (Thorpe et al., 2009).

Vertical climb and descent is slightly more associated with feeding than travel as was found in Sumatra (Thorpe and Crompton, 2005), and is more associated with single supports. However, the use of multiple supports for vertical climb/descent is more frequent during feeding than during travel (Table 2.7). This is the opposite pattern to the results for Sumatra where orangutans showed a preference for climb/descent on single supports during feeding (Thorpe and Crompton, 2005). In this study vertical scramble was more commonly observed when travelling in the crown of a feeding tree and this mode, by definition, involves multiple supports (Hunt et al., 1996). Vertical climbing is the most energetically costly form of locomotion particularly for a large bodied animal such as an orangutan, because it involves directly opposing gravity (Taylor et al., 1972; Cartmill, 1972, 1974; Cartmill and Milton, 1977). This is particularly important in the Sabangau forest were orangutans are frequently subjected to prolonged periods where they are in negative energy balance (Harrison et al., 2010). Vogel et al. (2009) suggest that there will be an expected increase in the

frequency of vertical climbing in rugose habitat given the large gaps between emergent trees. Rugosity is a measure of the irregular internal structure of a canopy; the canopy is more continuous when rugosity is small, but when rugosity is high there is a tendency for foliage to be concentrated lower in the canopy ((Vogel et al., 2009). However, as a consequence of past logging disturbance in the Sabangau, the continuous middle canopy now forms the main canopy and it is likely that this is the reason why climbing was observed at similar levels to that found in previous studies (Table 2.4, Thorpe and Crompton, 2006). Vertical climb and descent had a very negative association with travel in the peripheral strata (Table 2.7) and it would therefore appear that orangutans climb the taller trees in order to access the higher quality foods associated with them, thereby offsetting the energetic cost associated with climbing. Orangutans in disturbed peat-swamp forest, rather, utilised the lower, more continuous strata in order to reduce the energetic costs of locomotion.

Models which differentiated between pronograde and orthograde behaviour were also found to be highly significant during the modelling process, and while they did not produce the best model overall the distinction between pronogrady and orthogrady within the models produced three out of the top five models of best fit (Table 2.3). In addition, model 3 in Table 2.3, had the same variable relationships as the best fitting model in the analysis with the strongest association being locomotion * behaviour * no. supports, which was almost ten times stronger than the next variable association. Orientation of the body is particularly interesting as all living apes are arboreally orthograde, and pronograde suspension has been identified as the only mode that distinguishes orangutans from other living

apes (Thorpe and Crompton, 2006). It is therefore informative to study this relationship in more detail in order to understand how locomotion in terms of the orientation of the body is influenced by behaviour and the number of weight bearing supports (Table 2.10). Orthograde behaviour combined both suspension and bipedalism, but the majority of these observations were of orthograde suspension, only 5% of all observations being of bipedalism. Orthogrady was found to have a negative association with single supports during travel and with multiple supports during feeding.

Table 2.10 – Contingency Table for Model: locomotion * behaviour * no. of supports[a]

		Behaviour		
No. of Supports	**Locomotion**	**Feed**	**Travel**	**Total**
1	Pronograde	24.4 (13.7)	75.6 (13.0)	(13.2)
		0.2	*-0.1*	
	Orthograde	43.0 (40.7)	57.0 (16.6)	(22.3)
		6.1	*-3.4*	
	Climb/descent + Oscillation	16.6 (45.6)	83.4 (70.4)	(64.6)
		-3.7	*2.0*	
Total		23.5	76.5	100
>1	Pronograde	18.1 (19.1)	81.9 (10.3)	(11.3)
		3.2	*-1.1*	
	Orthograde	6.1 (39.7)	93.9 (73.6)	(70.0)
		-5.0	*1.7*	
	Climb/descent + Oscillation	23.5 (41.2)	76.5 (16.1)	(18.8)
		7.2	*-2.5*	
Total		10.7	89.3	100

[a] For explanation of table, see Table 2.6

Torso pronograde suspension was observed at much lower frequencies both in this study (1.3%), and in Cant's (1987b) study on another Bornean orangutan subspecies (*P. p. morio*, 1%) than was found in Sumatran orangutans (4%, Thorpe and Crompton 2006). This may suggest that Bornean orangutans exhibit pronograde behaviour at lower levels than their

Sumatran counterparts. Indeed, quadrupedalism was also observed at a higher frequency in Thorpe and Crompton's (2006) study of the Sumatran species compared to Cant (1987b) and this study, although Cant (1987b) had similar frequencies for travel but much lower frequencies for feeding. Thorpe and Crompton (2005, 2009) found that torso pronograde suspensory locomotion had an association with multiple small supports which would indicate that it is not the lack of suitably large supports in the Sabangau forest limiting the capacity for this type of locomotor behaviour. Although they also found that compressive quadrupedalism was more likely to occur on single large supports and this could suggest that there is a lack of strong enough supports for quadrupedalism in the Sabangau, particularly for adult males. Therefore, the reasons underlying the difference in pronograde locomotor behaviour between Sumatran and Bornean species are not yet clear. While they could reflect differences in forest structure and the availability of supports, they could also reflect a difference in locomotor behaviour at the species level.

The two studies compared in this manuscript reflect not only two different orangutan species but also two extremes in terms of forest structure: Ketambe consists of tall pristine dry forest with a sparse understorey and a more continuous upper canopy. The Sabangau forest, on the other hand, encompasses different stages of regeneration, thus a very dense understorey and a discontinuous upper canopy exists. While no detailed study of forest structure has been undertaken we might expect that the Sabangau, given its logging history, represents a extreme end of the spectrum of peat-swamp forests as the gaps in the upper canopy are emphasised with a very high density of small trees forming the understorey. While it is expected that

habitat structure, rather than forest type *per se*, determines locomotor behaviour, different forest types are typified by different habitat structures. Therefore, while the results of this study reflect the locomotor behaviour of orangutans in forest which is at one end of the gradient of habitats that extant orangutans inhabit, it is interesting that the orangutans exhibited the same range of behaviours as were found in forest at the other end of the gradient (Thorpe and Crompton, 2006) but at different frequencies. This highlights the need for a more in-depth assessment of differences between orangutan species that controls for habitat structure in order to further our understanding of the evolution of locomotor diversity and the proximate causes of such diversity.

2.5 Conclusions

This analysis showed that orangutan locomotion is influenced by behaviour, height in the canopy, number of supports and age-sex class. Orangutans used different locomotion when feeding than when travelling although locomotion was modified according to support use, height and age.

Log-linear modelling showed that locomotion could be understood in terms of either suspensory and compressive locomotion or orthograde and pronograde locomotion as these combinations produced the best fitting models. We expected that age-sex class wouuld have a strong influence on locomotion but this was not the case as log-linear modelling showed that age-sex class has only a limited influence and was best described, for Bornean orangutans, in terms of either age or sex, although the former appeared in the top 3 best fitting models. Orangutans in Sabangau used

multiple supports at a similar frequency to those in mixed dipterocarp forest, which was attributed to the high levels of tree-sway observed in this population. There was also a higher frequency of suspensory locomotion compared to orangutans in mixed dipterocarp forest. However, orangutans in disturbed peat-swamp forest did travell lower than was found in mixed dipterocarp forest. As we expected, orangutans exhibited much higher levels of oscillatory locomotion in this study, which is a possible consequence of previous forest disturbance resulting in a much greater density of small, compliant trees.

CHAPTER 3

Support use of wild orangutans (*P. p. wurmbii*) in disturbed peat swamp forest, Sabangau, Central Kalimantan.

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ABSTRACT

As orangutan habitats continue to be altered through human disturbance, examining how orangutans interact with their environment during locomotion in logged forest is fundamental to understanding how positional behavior relates to forest structure in the most arboreal great ape. This study examined the number, size and types of arboreal supports used during locomotion for a population of Bornean orangutans (*P. p. wurmbii*) in an area of disturbed peat-swamp forest (Sabangau Catchment, Indonesia). Backward elimination log-linear modelling was used to expose the main influences on locomotion. Our results found that in contrast to orangutans in dry-lowland forest (Thorpe and Crompton, 2005) the relationship between locomotor repertoire and support type and diameter (weighted by number of supports) was relatively weak. The way in which orangutans used the small tree trunks typical of this habitat suggests they fulfil a functional role provided by lianas in more pristine forest. In Sabangau, height in the canopy had a strong influence on support use, orangutans tended to use tree trunks below 10 m and branches and boughs above 10 m, although this appears to be a consequence of support availability in different strata. Body size had a limited influence on support use and whilst adult males are possibly too large to use single small supports, our results support previous suggestions that adult females are more cautious in their locomotor behavior than other age-sex classes. Overall our results suggest substantial differences in support use during locomotion between orangutans living in different habitats, highlighting the flexibility of their positional behavior.

3.1 Introduction

THE forest canopy is an inherently complex and demanding environment in which to move (Warren, 1997). The three-dimensional structure of branches, boughs and lianas, which are of varying strength, size, length, orientation, flexibility, abundance and spatial distribution, provide a constantly changing environment through which arboreal animals must negotiate their travel and feeding paths. The characteristics of supports within the canopy have been shown to have substantial influence on the expressed locomotor repertoire of many arboreal primates (e.g. Ripley, 1967; Fleagle, 1978; Crompton, 1984; Cartmill, 1985a; Cant, 1987b; McGraw, 1996; Thorpe and Crompton, 2005). Efficient travel through the canopy is constrained not only by the animal's ability to use available supports but also by their ability to cross gaps in the canopy (Temerin and Cant, 1983; Cant, 1988). Open space within the canopy is a normal feature of tropical forest as a result of natural tree falls. However, logging increases both the size and number of gaps in the canopy. Furthermore, tree branches are tapered, and as they stretch outwards towards their periphery, they become smaller, weaker and less stable (Grand, 1972). When they are loaded with an animal's body mass they can deflect considerably, thus increasing the effective size of a gap. Lianas are therefore an important structural component of tropical forests because they often link trees together, providing pathways across small gaps for arboreal animals (Emmons and Gentry, 1983). However larger gaps remain a problem and the ability to cross canopy discontinuities is extremely important for efficient arboreal travel as individuals may otherwise be forced to descend to the ground or travel longer distance around a gap, thereby increasing energy expenditure on locomotion (Cant, 1992; Felton et al., 2003; Thorpe et al., 2007a).

Orangutans are the largest arboreal primate (Cant, 1987b) and show extreme sexual dimorphism. Flanged males weigh between (80-91kg), which is more than twice that of adult females (33-45kg) (figures based on Bornean orangutans only. Markham and Groves, 1990). Unflanged males are of a similar size or larger than adult females and adolescents weigh around 15kg (Manduell, unpublished data). Given their large body size and the degree of variation between age-sex classes, orangutans are undoubtedly an interesting species in which to investigate the relationship between locomotion and support use. Although orangutans inhabit a wide range of habitats in both primary and secondary forest types (Rodman and Mitani, 1987; Knott, 1999; Morrogh-Bernard et al., 2003; Husson et al., 2009), to date the only detailed studies of orangutan positional behavior have taken place in dry-lowland forest and logged peat-swamp forest (Thorpe and Crompton, 2005, 2006, 2009; Thorpe et al., 2007a, b, 2009; chapter 2). These two forest types are structurally very different, dry-lowland forest having a taller canopy (around 45 m, Whitmore, 1984) and a higher density of large trees and established lianas, in addition to an increased variety of support sizes and types (chapter 4). In contrast, disturbed peat-swamp forest is more stunted with a canopy height of around 15 m to 25 m (Page et al., 1999). The forest structure is much more homogeneous with a high density of small trees, few large trees and established lianas, and a much more limited abundance of large branches (chapter 4). The response of primates to variations in habitat structure, and their ability to either adapt, or maintain consistency in their locomotor behaviour is both interesting and important, particularly as forest structure continues to be altered through human disturbance (chapter 4). Thus in order to better understand the relationship between orangutan locomotion and support use it is necessary to examine

the limits, or indeed plasticity, of locomotor/support combinations in forests which are fundamentally different in terms of their structure.

Numerous studies have addressed the issue of habitat structure and support use by arboreal primates, yet despite this, the extent of the influence of forest structure on primate locomotion is still not well understood (e.g. Garber and Pruetz, 1995; McGraw, 1996, 1998, 2000; Dagosto and Yamashita, 1998; Garber, 1998; Remis, 1998; chapter 4). We would expect animals to exploit supports that enable them to move most efficiently through the canopy (Prost, 1965). However, whether supports are selected as a consequence of their prevalence in the environment or whether they are selected for characteristics that facilitate certain behaviours is likely to differ between primate species as a result of influences such as locomotor anatomy, body size, group size, social rank, foraging strategy, as well as structural diversity of the canopy (Garber, 1998). Inter-specific comparisons of wild orangutan locomotion found the overall repertoire of orangutan locomotor behavior to be similar between species; although there were differences in the relative frequencies of observed modes. In disturbed peat-swamp forest, orangutans tended to exhibit higher frequencies of a relatively small number of behaviours compared to the repertoire observed in dry-lowland forest (Thorpe and Crompton, 2006; chapter 4). However, aside from a stronger tendency for orangutans in dry-lowland forest to use lianas, orangutans in the two forest types did not differ substantially in their preferred supports (chapter 4). Therefore, we might expect orangutans in disturbed peat-swamp to use similar locomotor/support combinations (e.g. quadrupedal walking on stiff branches) as was observed in dry-lowland forest (Thorpe and Crompton, 2005), with the exception of the use of lianas.

Differences in frequencies of observed locomotor behavior are likely to reflect the vast differences in forest structure and support availability between the two forest types. Despite the general similarity in preferred supports for locomotion between Bornean and Sumatran orangutans, previous studies in dry lowland forest have found significant differences in support use between different age-sex classes. Adult male orangutans selected supports that were larger and stiffer for feeding postures than any other age-sex class (Myatt and Thorpe, 2011), as might be expected. However, they did not select stiffer supports for locomotion, rather it was adult females who utilized supports that were more stable and secure (Thorpe et al., 2009). The latter result was attributed to adult females becoming more conservative in their locomotion after parturition (Thorpe and Crompton, 2005; chapter 4). However, in disturbed peat-swamp, with its limited abundance of large arboreal supports, it is possible that there is greater mass-related variation in support use during locomotion than was observed in dry-lowland forest.

No study has yet fully established the relationship between support use and locomotion for Bornean orangutans, or for orangutans inhabiting logged peat-swamp forest. Thus, the primary aim of this study is to build on previous work (chapter 2) through a comprehensive study of support use during locomotion by a population of wild orangutans (*Pongo pygmaeus wurmbii*) inhabiting an area of disturbed peat-swamp. In this study we will test the association between support characteristics (diameter, type and number of supports used), locomotion, age-sex category (as a correlate of body mass) and height in the canopy. Specifically, we hypothesize that 1) orangutans in this study will use the same locomotor/support combinations

as those found in dry forest (Thorpe and Crompton, 2005) given the similarity in preferred supports. This leads to hypothesis 1a) that differences in observed frequencies of locomotor behavior will directly reflect differences in support availability between the two forest types (chapter 4); 2) orangutans in this study will exhibit greater mass-related variation in locomotion and support use than was observed in Thorpe and Crompton's (2005) study, given the limited availability of large branches (chapter 4); 3) height in the canopy will not have a strong association with support characteristics used during locomotion, given the stunted, homogeneous forest structure; 4) the high abundance of small trees typical of disturbed peat-swamp fulfil a functional role provided by lianas in more pristine habitat given their vertical orientation, small girth and therefore compliant nature, and orangutans were found to have a preference for lianas in more pristine habitat, but not in logged peat-swamp (chapter 4).

3.2 Methods

Field Study

The study was conducted in a 4km^2 area of disturbed peat swamp forest between March and September 2007 and April 2009 and January 2010. Field research was carried out in collaboration with the OUTROP-CIMTROP multi-disciplinary research project within the LAHG (Laboratorium Alam Hutan Gambut: Natural Laboratory for the Study of Peat Swamp Forest), a 500km2 area of forest located at the northern end (02°19'S, 113°54'E) of the Sabangau. The research area has been described in detail by Page et al. (1999).

Orangutans (*Pongo pygmaeus wurmbii*) in the LAHG have been studied continuously since 2003 and are thus known and habituated to observers. All observations were made by a single observer (KLM) during nest-to-nest follows of wild orangutans, in order to ensure consistency. Self-training in the estimation of locomotor behaviors, heights and support diameters (Table 3.1) was undertaken prior to the collection of data and further training in estimating height and diameter was carried out during the data collection period in order to maintain accuracy. The classification of positional behavior follows that detailed by Hunt et al. (1996) but also includes additional positional modes described by Thorpe and Crompton (2006) for orangutans. Once an orangutan was found it was followed until it made its night nest (15:00h – 19:00h), the nest was returned to the following morning before dawn (04:30h) and the focal individual followed from nest-to-nest for a period of up to 10 days within a given month. Wherever possible, individuals were followed on more than one occasion in order to remove any bias caused by temporarily abundant fruit, although it was not always possible to locate the same individuals again. Data were collected using focal instantaneous sampling on the 1-min mark, using a digital watch with a countdown-return vibration alarm function. Details of data collected at each sample point are presented in Table 3.1.

Twenty-two individuals were observed, including all age-sex categories (see Appendix A, Table A.1). Adult males or flanged males were defined as those possessing secondary sexual characteristics such as cheek flanges, larger body size and throat pouches, whereas sub-adult males or un-flanged males were those that showed sexual activitiy but did not possess secondary sexual characteristics. Adult females were classed as those that had

Table 3.1 – Positional Behaviour Observations[a]

1. **Date**
2. **Individual**
3. **Time**
4. **Positional mode**[b]
   1. Quadrupedal Walk: Locomotion on top of supports angled at <45° of true horizontal; typically all four limbs contact the support in a particular sequence. The torso is pronograde (–) or roughly parallel to the support. Includes tripedal walk, quadrupedal run, and tripedal run.
   2. Bipedal Walk: Hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. Includes flexed and extended bipedalism, and hand-assisted bipedalism in which hindlimbs bear more than 50% of body mass, but one or both forelimbs are used to assist, either in suspension or compression, and bear more than their own weight.
   3. Climb/descent: Ascent and descent on supports angled at ≥45°. Distinction is made between vertical climb/descent (within 20° of true vertical) and angled climb (between 20° and 45° of true vertical).
   4. Torso-orthograde suspension: Includes brachiation and orthograde clamber which is a forelimb suspensory torso-orthograde mode (|), but with hindlimbs assisting. All the four limbs act as propulsors, with most body weight borne by the abducted forelimbs. Also includes the mode drop, in which all pre-drop postures were orthograde in nature.
   5. Torso-pronograde suspension[c]***:*** All the four limbs are used in some combination; the torso is pronograde, and limbs are in tension.
   6. Bridge[c]***:*** A torso-pronograde gap-closing movement where the hands reach out to grasp a support on one side of a gap and cautiously pull the body across the open space with the feet retaining their grips until a secure position is established on the other side . A gap is therefore defined for this purpose as where there is open space between the peripheral branches of neighbouring trees.
   7. Oscillation: Combines modes tree sway and ride. Tree sway is a gap crossing movement used between trees where either body weight or oscillation are used to deform branches, and often the pre-gap closing posture resembles clinging more than suspension. Ride is similar to tree sway, but is used from tree to ground, although it can also be used to move from a higher to a lower level in the canopy as in Thorpe and Crompton (2005). A small diameter support is grasped in a clinging posture and a movement or oscillation overbalances the support. The weight of the individual's body pulls the support from a vertical orientation toward horizontal. As the support approaches horizontal a suspensory posture may result, after or during which the grip with the hindlimb is released and the feet contact the ground/support(s) at a lower level in the canopy.
5. **Height:** 5m intervals up to 30m, >30m (measured as the vertical distance from the animal to the ground).
6. **Number of Supports:** 1, 2, 3, 4, >4.
7. **Support Type:** Trunk (the main axis of a tree); Bough (primary stem arising from the trunk); Branch (secondary stem arising from a bough or other branch); Liana (woody vine); Other (aerial roots, nest).
8. **Support Diameter:** <2cm; ≥2 - <4cm; ≥4 - <10cm; ≥10 - <20cm; ≥20 - <40cm; ≥40cm.

[a] Data collection followed Thorpe and Crompton (2005)

[b] All follow those of Thorpe and Crompton (2006), which were based on Hunt et al. (1996).

[d] For analysis, pronograde suspension and bridge were conflated, as both had very small frequencies and are functionally similar.

produced offspring or were old enough to have had produced offspring. Adolescents were individuals that were independent but did not show sexual activity (Rijksen, 1978). Thirty-six percent of all observed locomotor bouts sampled behavior of adolescent males and females (four individuals), 30% sampled adult or flanged males (eight individuals), 17% sub-adult or unflanged males (five individuals) and 17% adult females (five individuals).

Statistical Analysis

The interdependence of observations presents a particular problem in the analysis of positional behavior, as sequential observations using small time intervals are considered to be highly dependent (Mendel, 1976; Janson, 1984; Hunt, 1992; Dagosto, 1994; McGraw, 1996; Warren and Crompton, 1997; Cant et al., 2001; Thorpe and Crompton, 2005). However, wild orangutans spend very little time in locomotion; pause frequently during bouts of travel and visibility is often impaired due to the dense foliage thereby reducing the number of sequential observations (Thorpe and Crompton, 2005; chapter 2), therefore the dependence of datapoints in this study was considered negligible and all locomotor observations were analyzed (after Thorpe and Crompton, 2005 and chapter 2).

Backward elimination log-linear modeling is a useful tool in the analysis of categorical data as it allows the analysis of multiway contingency tables. We examined multiple relationships between locomotion, support type and support diameter, both of which incorporated data on the number of supports used, with regard to age-sex category and height in the canopy, using SPSS version 15.0. Note that it was necessary to model the effects of height and age-sex on locomotion and support use separately because

multivariate statistics require far larger datasets than are generally obtainable for locomotion under field conditions (Thorpe and Crompton, 2005). Log-linear analysis also allows significant interactions between categorical variables to be ranked in order of their relative importance and it does not require the data to come from a normally distributed population (Crook, 1997). A significance value of 1 for the $\chi 2$ likelihood ratio indicates a perfect fit of the model's predicted cell counts to the observed cell counts, although a P value of >0.05 is considered significant (Agresti, 1990; Thorpe and Crompton, 2005; Thorpe et al., 2007b). For more detailed information on this technique and the model selection process refer to Thorpe and Crompton (2005) and chapter 2.

The variable interactions (i.e. model expressions) produced by log-linear models can be analysed in more detail to investigate the nature of associations between variables through contingency tables containing row and column percentages and standardised cell residuals (SCRs). Standardised cell residuals indicate by their sign whether an interaction is more (positive values) or less (negative values) common than predicted by the model and, by their size, to what degree. Standardised cell residuals greater than ±2 indicate a substantial variation from the model predictions and therefore may be of particular interest (Thorpe et. al., 2007b). In addition, odds ratios may be used to aid in the interpretation of patterns in the data as they represent ratios of probabilities and can thus be used to establish correlations which underlie significant associations (Crook, 1997).

An additional benefit of log-linear analysis is that it may be used to determine whether the distribution of the data can be explained by a

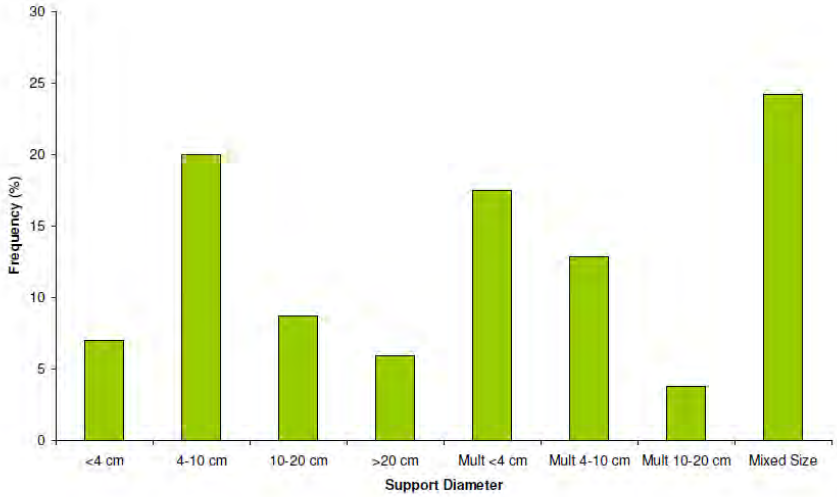
simpler, underlying structure. Thus we conflated variables to find the simplest way to classify the data whilst producing models of good fit (chapter 2, Table 2.2, pg 47). Locomotor modes were conflated based on broad biomechanical similarities following Thorpe and Crompton (2005). Support type and support diameter were conflated in a manner which allowed the number of supports to be included in the classification, for example, diameter: single <4cm and type: multiple trunk (after Thorpe and Crompton, 2005). Structural zeros (i.e. combinations that cannot possibly happen) resulting from the incorporation of the number of supports within the support type and diameter variables can be accounted for in the models. For example, if an observation of locomotion was on a single trunk (support type), then it cannot have taken place on multiple supports <4 cm or multiple supports >4 cm (support diameter) and is therefore a structural zero. Models for all combinations of variables were examined and then ranked in order of P-value.

3.3 Results

Descriptive Statistics

A total of 18,220 instantaneous observations of positional behavior were recorded, of which 2,874 were of locomotion. Of the locomotor observations, 2,037 included full information on the types of supports and their respective diameters. Single supports of >4 cm were the most commonly used support diameter, accounting for 36.5% of all observations, whereas single supports of <4 cm were the least used support diameter accounting for only 6.2% of all observations (Figure 3.1). Support types used were more evenly distributed although trunks (both single and multiple)

Figure 3.1 – Frequency of Support Diameters Used During Locomotion

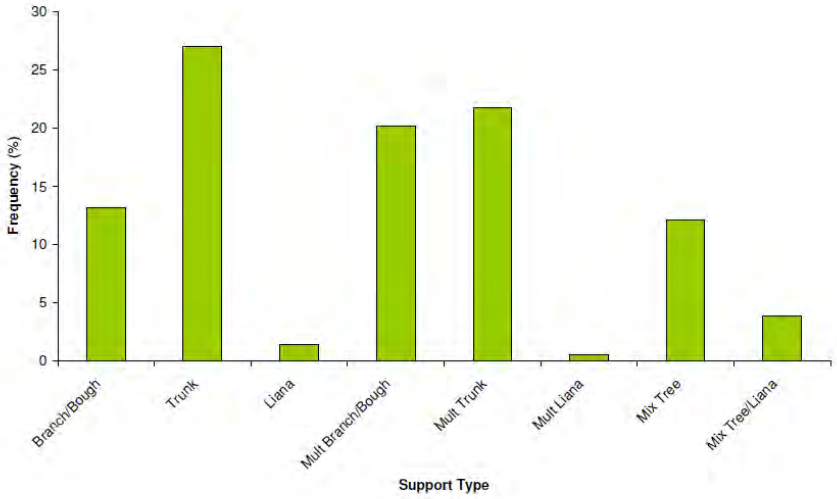


were the most commonly used supports (Figure 3.2). The use of lianas accounted for such a small proportion of the supports used (3.8%) that they were unable to be incorporated into the analysis as they resulted in unacceptable levels of sampling zeros.

Model Interpretation

Locomotion was best explained in terms of compressive or suspensory behavior or vertical climb/descent and oscillation (tree-sway), which involve a combination of compressive and suspensory postures. Support diameter was best explained in terms of <4 cm and >4 cm and support type was best explained in terms of branches and boughs combined, tree trunks and mixed supports (i.e. trunks with either a branch or a bough, or both). Both support diameter and support type incorporated information on whether supports were either single or multiple.

Figure 3.2 – Frequency of Support Types Used During Locomotion



A comparison of the standardized χ^2 values associated with the interactions of the different variables with locomotion in the two models (Table 2.5) indicate that all tested variables, with the exception of height, do influence orangutan locomotion in disturbed peat-swamp to some extent. Each of these models together with the associated variable relationships is discussed in turn.

Model Variables: height * locomotion * support type * support diameter

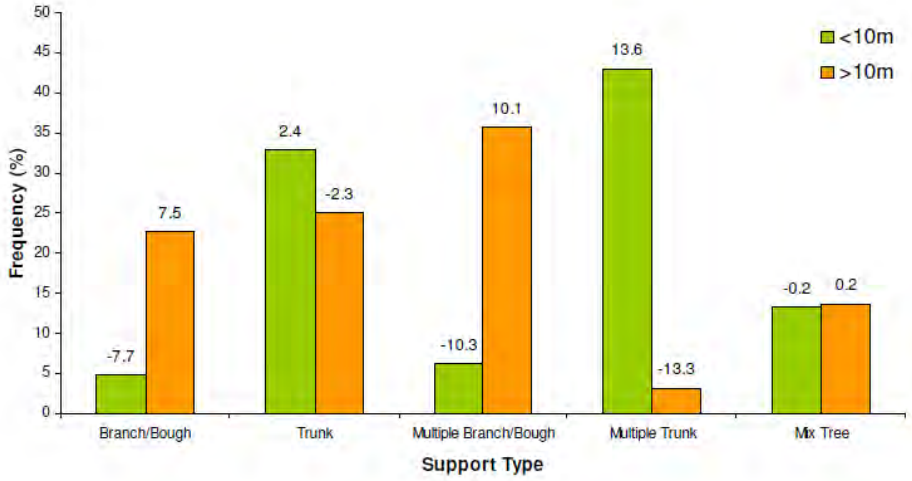
The strongest association in the model was between height and support type which was 11 times stronger than the association between height and support diameter and 30 times stronger than the association between locomotion, support diameter and support type (Standardized χ^2 values, Table 3.2). Both single and multiple branches/boughs had a positive association with locomotion above 10 m (SCRs = 7.5 and 10.1, respectively;

Table 3.2 – The statistically best-fitting models

Model	Model Expressions [1]	Partial χ^2	Degrees of Freedom	Significance Level	Standardised χ^2 (χ^2/degrees of freedom)
Subset A	**height, locomotion, diameter, type**	**18.571**	**22**	**0.672**	
Height	height * type	445.521	3		148.51
	height * diameter	39.34	3		13.11
	locomotion * diameter * type	38.962	8		4.87
Subset B	**age-sex, locomotion, diameter, type**	**20.709**	**26**	**0.757**	
	age-sex * diameter	25.216	3		8.41
	age-sex * locomotion	14.609	2		7.3
	age-sex * type	18.055	3		6.02
	locomotion * diameter * type	44.041	8		5.51

[1] Height: <10 m, >10 m; Age-sex: adult male + adult female, subadult male + adolescents; Locomotion: compression, suspension, vertical climb/descent + oscillation; Diameter: <4 cm, >4 cm, multiple <4 cm, multiple >4 cm, Mix (<4 cm, >4 cm); Type: branche/bough, trunk, multiple branch/bough, multiple trunk, mixed (branch/bough/trunk)

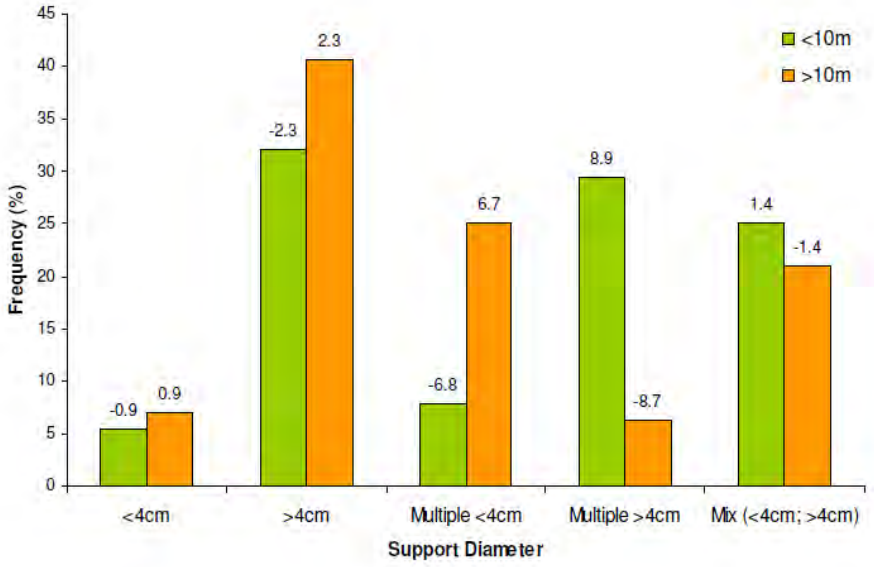
Figure 3.3 – Variable Interaction: Height * Support Type



* *Figures are standardised cell residuals*

Figure 3.3) whereas both single and multiple trunks had a positive association with locomotion below 10 m (SCRs = 2.4 and 13.6, respectively; Figure 3.3). Indeed travel on multiple trunks was 9 times more likely to occur below 10 m than above 10 m, and travel on multiple branches and boughs was 9 times more likely to take place above 10 m than it was below 10 m (odds ratios). The association between height and diameter Figure 3.4 shows that orangutans used multiple supports of >4 cm more than expected below 10 m, but less than expected above 10 m (SCRs = 8.9 and -8.7, respectively). However, the reverse pattern was observed for the use of multiple supports <4 cm, which had a negative association with locomotion below 10 m and a positive association with travel above 10 m (SCRs = -6.8 and 6.7, respectively). Finally, locomotion on single supports >4 cm had a positive association above 10 m but not below 10 m (SCRs = 2.3 and -2.3, respectively).

Figure 3.4 – Variable Interaction: Height * Support Diameter



* *Figures are standardised cell residuals*

The association between locomotion, support type and support diameter was the weakest relationship in this model, but was retained in both subset models (Table 3.2). This relationship is presented in Table 3.3. Compressive locomotion was strongly associated with single branches/boughs of the largest size category (SCR = 7.7) and was 15 times more likely to take place on single branches/boughs >4cm diameter than on single branches/boughs <4 cm (Table 3.3, column percentages). Suspensory locomotion took place on single branches/boughs of both size classes more often than predicted by the model, although it was observed at similar frequencies for both size categories (Table 3.3, column percentages). All three locomotor behavior categories showed a positive association with single trunks >4 cm. Multiple trunks were classified as a structural zero for compressive locomotion as, whilst single tree falls were used for compressive locomotion, the vertical

orientation of tree trunks precluded multiple tree trunks from being used during compressive locomotion. Both suspensory locomotion and climb/descent and oscillation had a positive association with multiple tree trunks >4 cm. All three locomotor behavior categories had a strong association with mixed supports of mixed size (<4 cm; >4cm), although this was strongest for climb/descent and oscillation. In addition, all three locomotor behavior categories had a strong relationship with multiple branches/boughs <4 cm. However, only climb/descent and oscillation had a positive association with multiple branches/boughs >4 cm (SCR = 7.5).

Model Variables: age-sex * locomotion * support type * support diameter

The strongest association in this model was between age-sex and support diameter, however this was only marginally more important than the other relationships in the model. The only major difference in the diameter of supports used by the different age-sex categories was that adult males and adult females used single supports <4cm less than predicted whereas the converse was true for subadult males and adolescents (SCRs = -2.4 and 2.3, respectively; Figure 3.5). In fact, subadult males and adolescents were 2.3 times more likely to use single small supports (<4cm) for locomotion than adult males and adult females. No major pattern was apparent for the SCRs for the remaining 2-way associations in this model (age-sex * locomotion and age-sex *support type), therefore these associations are not presented here. The relationship between locomotion, support type and support diameter (Table 3.3), was also the weakest association in this subset.

Table 3.3 – Contingency table for model expression: locomotion * support diameter * support type

		Support Type					
Locomotion	**Support Diameter**	**Branch/Bough**	**Trunk**	**Multiple Branch/Bough**	**Multiple Trunk[4]**	**Mix**	**Total**
Compression[2]	<4 cm	50.0 (6.3)	50.0 (7.7)	-	-	-	1.9
		1.8	*2.2*	-	-	-	
	>4 cm	55.6 (93.8)	44.4 (92.3)	-	-	-	25.4
		7.7	*6.8*	-	-	-	
	Multiple <4 cm	-	-	94.7 (64.7)	-	5.3 (31.3)	44.6
		-	-	*3.6*	-	*-0.8*	
	Multiple >4 cm	-	-	76.9 (7.2)	-	23.1 (18.8)	6.1
		-	-	*0.5*	-	*2.0*	
	Mix (<4 cm; >4 cm)	-	-	83.0 (28.1)	-	17.0 (50.0)	22.1
		-	-	*1.5*	-	*2.4*	
	Total	15.0	12.2	65.3	-	7.5	100.0
Suspension[3]	<4 cm	95.9 (41.7)	4.1 (21.1)	-	-	-	9.6
		15.4	*1.6*	-	-	-	
	>4 cm	89.7 (58.3)	10.3 (78.9)	-	-	-	14.4
		17.3	*7.4*	-	-	-	
	Multiple <4 cm	-	-	82.5 (78.7)	13.9 (5.2)	3.6 (4.0)	16.5
		-	-	*20.2*	*-5.8*	*-3.7*	
	Multiple >4 cm	-	-	1.0 (1.7)	98.4 (67.7)	0.7 (1.3)	30.3
		-	-	*-6.8*	*14.3*	*-6.4*	
	Mix (<4 cm; >4 cm)	-	-	11.5 (19.5)	40.7 (27.1)	47.8 (94.6)	29.3
		-	-	*-2.4*	*-0.8*	*14.7*	
	Total	22.1	1.9	17.3	43.9	14.8	100.0
Climb/Descent + Oscillation	<4 cm	30.8 (27.5)	69.2 (3.3)	-	-	-	3.2
		7.4	*0.2*	-	-	-	
	>4 cm	3.9 (72.4)	96.1 (96.7)	-	-	-	66.7
		0.4	*8.5*	-	-	-	
	Multiple <4 cm	-	-	92.5 (61.7)	3.8 (17.6)	3.8 (2.8)	9.8
		-	-	*18.1*	*1.0*	*-2.4*	
	Multiple >4 cm	-	-	60.0 (20.0)	32.5 (76.5)	7.5 (2.8)	4.9
		-	-	*7.5*	*13.3*	*-1.0*	
	Mix (<4 cm; >4 cm)	-	-	17.5 (18.3)	0.8 (5.9)	81.7 (94.5)	15.4
		-	-	*0.8*	*-1.0*	*21.0*	
	Total	3.6	66.3	14.7	2.1	13.4	100.0

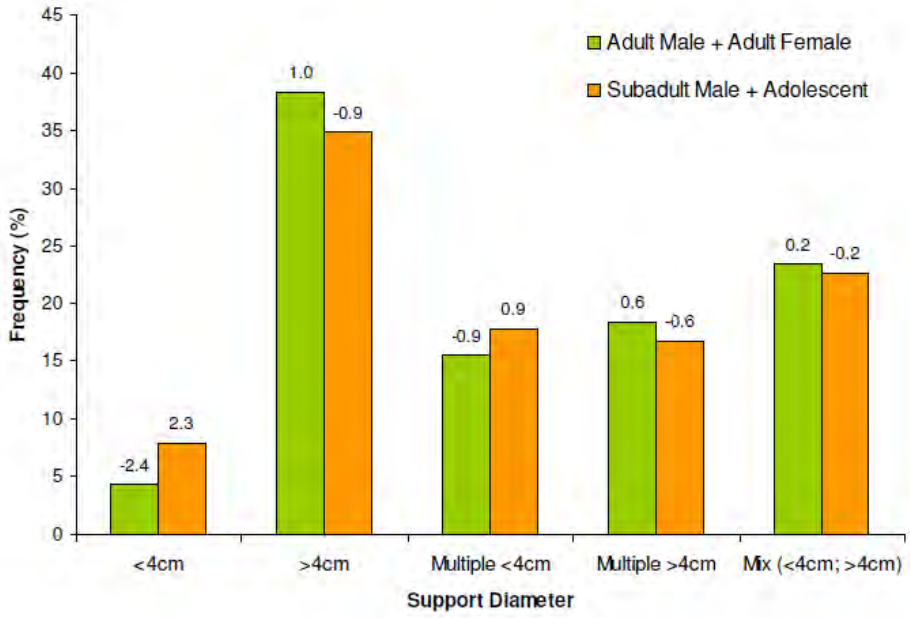
[1] Entries are row % and (column %) for each locomotion*support type * support diameter unit, e.g., 50% of all compressive locomotion on single supports <4 cm was on single branches/boughs and 6.3% of all compressive locomotion on single branches/boughs was on <4 cm diameter supports. Standardised cell residuals are in italics (negative values indicate frequency is lower than expected). - denotes structural zeros which are omitted from the modelling procedure and do not affect the accuracy of the model.

[2] Compression includes the modes bipedal, tripedal and quadrupedal walk.

[3] Suspension includes the modes torso-orthograde suspension and torso-pronograde suspension.

[4] It must be noted that whilst single trunks were retained in the model, multiple trunks were classed as structural zeros for compressive locomotion. This is due to the fact that trunks are vertical supports and while compressive behaviour was observed on fallen tree trunks it was not observed on multiple fallen tree trunks which are not typically available as a support type in this forest.

Figure 3.5 – Variable Interaction: Age-Sex * Support Diameter



* *Figures are standardised cell residuals*

3.4 Discussion

The habitat structure and support availability of peat-swamp forest is vastly different to that of dry lowland forest (chapter 4). Not only that, but the prolonged history of disturbance in Sabangau has resulted in an even more stunted canopy, characterized by an extremely high density of smaller trees (Table 3.4; chapter 4). Indeed, Sabangau contained over three times the density of trees below 40 cm DBH (diameter at breast height, 1.3 m) than Ketambe; whereas Ketambe had four times more trees above 40 cm DBH than Sabangau (Table 3.4). In addition, Sabangau had a significantly lower density of all lianas larger than 2 cm in diameter than Ketambe (Table 3.4). The abundance of larger branches and boughs was also significantly higher in Ketambe (Table 3.4), further highlighting the more heterogeneous

structure of dry lowland forest compared to disturbed peat-swamp. However, despite these great differences in forest architecture, orangutans in both forest types have been found to have similar profiles in preferred supports, with the exception of liana use (chapter 4). This led us to predict (hypothesis 1) that orangutans share locomotor/support preferences regardless of forest type; but that habitat constraints in disturbed forest would limit orangutans to higher frequencies of fewer locomotor behaviors. However, the preference for lianas in more pristine forest, that are absent in disturbed peat-swamp also led us to predict that the high density of small compliant tree trunks in Sabangau might fulfil a similar functional role to that of lianas elsewhere (hypothesis 4). Finally, the homogeneity and stunted canopy of the Sabangau forest led us to predict that height in the canopy would have only a limited influence on support use (hypothesis 3), whereas the limited abundance of larger supports in Sabangau led us to predict that there would be greater mass-related variation in support use than was observed in dry lowland forest (hypothsis 2, Thorpe and Crompton, 2005).

Lianas are woody vines that are flexible in compression but strong in tension and comprise a large part of the plant community in the majority of tropical forests and play an important structural and ecological role, also providing food and arboreal pathways for many vertebrate species (Emmons and Gentry, 1983; Ghazoul and Sheil, 2010). In fact, the ability of Sumatran orangutans to access the canopies of large trees by using vertical lianas has been highlighted as an indication of their effectiveness in negotiating large, vertical supports compared to other Sumatran primates (Cant, 1992). Certainly, the use of lianas by orangutans played a particularly

Table 3.4 – Tree and liana densities with mean canopy variables and support abundance for trees >10 cm DBH

	Stem Density/ha^2	
Variable	**Ketambe**	**Sabangau**
Trees <4 cm DBH	1,182	4,505***
Trees ≥4 - <10 cm DBH	654	2,100***
Trees ≥10 -<20 cm DBH	249	687***
Trees ≥20 - <40 cm DBH	126	214***
Trees ≥40 cm DBH	67***	17
Lianas <2 cm DBH	1,025	924
Lianas ≥2 - <4 cm DBH	202**	121
Lianas ≥4 cm DBH	119**	53
	Mean	
Variable	**Ketambe**	**Sabangau**
DBH	29.69***	17.40
Crown Volume	270.11***	84.18
Crown Width (m)	7.47***	5.32
Tree Height (m)	20.33***	16.51
Bole Height (m)	10.7	10.5
Boughs <2 cm	15.43	14.67
Boughs 22 - 4 cm	10.22	9.45
Boughs 4 - 10 cm	6.57***	3.67
Boughs >10 cm	3.58***	0.45
Branches <2 cm	1,600.29***	892.06
Branches 2 - 4 cm	19.17**	8.08
Branches 4 - 10 cm	4.70***	1.80
Branches >10 cm	1.78***	0.03

Mann Whitney U-test: *P ≤ 0.05, **P ≤ 0.01; ***P ≤ 0.001, asterisks are placed on the site with the highest mean for each variable tested.

important role with regard to entering emergent feeding trees in dry-lowland forest (Thorpe and Crompton, 2005). In the present study, the use of lianas as supports during locomotion accounted for only 3.8% compared to 18.1% in Thorpe and Crompton's (2005) study, and thus had to be excluded from the analysis as a result of unacceptably high numbers of sampling zeros. Peat-swamp forest naturally has a lower density of lianas than dry-lowland forest because of the lower nutrient levels in peat soils (Whitten et al., 2000). However, the history of disturbance also influences liana density as lianas tend to be more prevalent in disturbed forest because most species need light, often from gaps in the canopy in order to germinate and establish (Ghazoul and Sheil, 2010). Ketambe certainly had a higher density of larger, well established lianas, whereas the densities of smaller, younger lianas were similar in both forests (Table 3.4). However, Cant et al. (1990) found that even lianas as small as 1.4 cm in diameter had the potential to support 1.25 times an adult male's body mass provided they were securely attached. Nevertheless, the lack of large trees in Sabangau means they seldom provide canopy pathways for arboreal primates. Cant (1992) suggested that in forest which has low densities of lianas, orangutans may be more capable of crossing gaps by tree-swaying using vertical trunks, and this certainly seems to be the case in the Sabangau, given the high frequency of trunk use and the high incidence of tree-sway compared to previous studies Thorpe and Crompton (2005).

Locomotion in disturbed peat-swamp forest was best understood in terms of compressive and suspensory locomotion, regardless of orientation of the torso. In this study, the best-fitting models were produced when locomotion was conflated into only three categories based on whether weight was borne

above (compression) or below (suspension) supports, or in combination (climb/descent and oscillation). Although Thorpe and Crompton (2005) found that these models also described orangutan locomotion in dry lowland forest well, their best-fitting models were obtained when distinction was made between a larger number of locomotor categories. This supports our suggestion that orangutan locomotion in Sabangau may be more restricted by the homogeneity of the logged, peat-swamp forest.

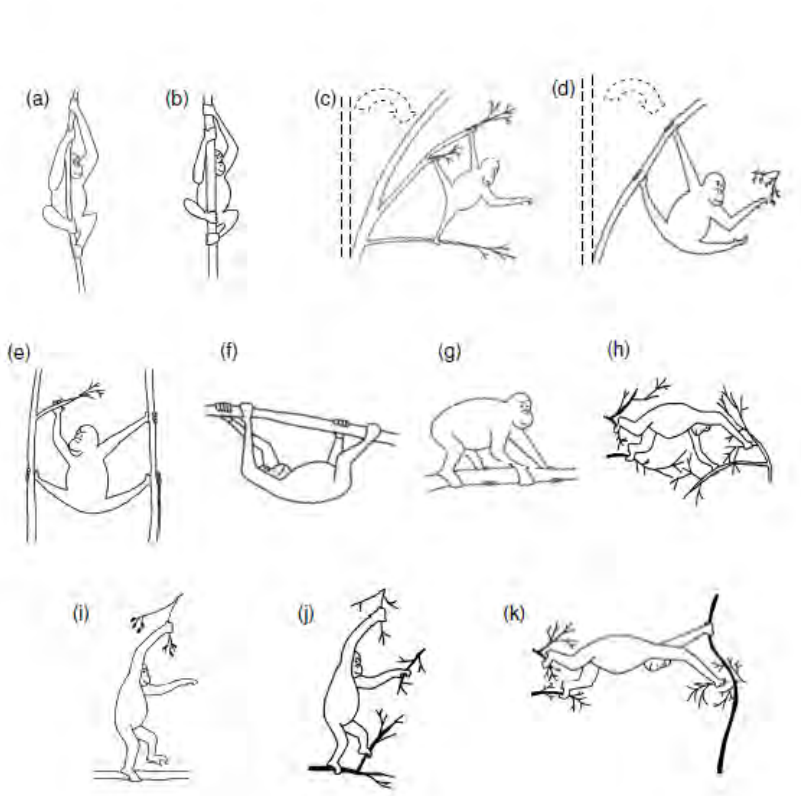
Vertical climbing and oscillation are, in terms of energetic cost, the most interesting of the orangutans locomotor behaviors. Vertical climbing opposes gravity and is energetically very expensive for large bodied primates, such as the orangutan (Hanna and Schmitt, 2011). In contrast, tree-sway has been shown to be a mechanism by which orangutans can lower energy expenditure on locomotion (Thorpe et al., 2007a). The types of supports used for vertical climb/descent and oscillation differed between the two sites. Oscillation in dry-lowland forest tended to involve the use of multiple small supports, whereas vertical climb/descent was strongly associated with the use of lianas (Thorpe and Crompton, 2005). In this study, whilst vertical climb/descent and oscillation had positive associations with a wider range of support types, they were most frequently observed on single tree trunks. Thorpe and Crompton (2005) found that orangutans in dry lowland forest preferred to climb lianas in order to enter large feeding trees, which may otherwise have been difficult to access (Figure 3.6a), however, in Sabangau the girth of tree trunks were typically sufficiently small for orangutans to climb directly (Figure 3.6b). That orangutans in Sabangau climb tree trunks, rather than using lianas, lends further support to our prediction that the smaller trunks of trees in

Sabangau fulfil a functional role provided by lianas in more pristine forest.

Oscillatory locomotion relies on the compliance of supports and is therefore restricted to those of a smaller diameter. In the Sabangau, 45% of all observations of tree-sway took place on single supports that were 4-10 cm in diameter, of which there were almost four times the density than in Ketambe. It would appear that the abundant small trunks in Sabangau enabled orangutans to tree-sway with body mass alone, whereas the use of multiple mixed supports in Ketambe suggests that as the trees are substantially larger, orangutans are required to distribute their mass over several connected supports and actively oscillate them in order to reach the magnitude of oscillations required to bridge gaps (Figure 3.6c and d). The incidence of tree-sway was also much higher in Sabangau than in Ketambe (chapter 2). Since tree-sway reduces the energetic cost of locomotion when compared to jumping across a gap or descending to the ground and climbing on the other side of a gap (Thorpe et al., 2007a), the increased frequency of tree-sway may alleviate some of the effects of habitat disturbance on the Sabangau population, which is known to be energetically stressed as a result of the low productivity of the forest (Harrison et al., 2010).

Our prediction that orangutans in disturbed peat-swamp forest will have the same locomotor/support combinations to those found in dry lowland forest was not upheld in this study. Thorpe and Crompton (2005) found that in dry-lowland forest, support type and support diameter (weighted by the number of supports) had the strongest association with locomotion. However, in Sabangau these relationships were relatively weak. Suspensory

Figure 3.6 – Common Locomotor Modes



(a) Flexed-elbow vertical climbing on a liana in Ketambe.
(b) Flexed-elbow vertical climbing usually involved a single tree trunk in Sabangau.
(c) Tree-sway using a single small tree trunk was common in Sabangau.
(d) Tree-sway in Ketambe often involved the use of multiple supports.
(e) Orthograde clamber frequently involved the use of tree trunks in Sabangau.
(f) Inverted pronograde walk was a rare behaviour in Sabangau.
(g) Symmetrical gail walk typically takes place on stiff supports and was more common in Ketambe.
(h) Pronograde scramble typically takes place on small, irregular placed supports.
(i) Extended bipedal walk was more commonly observed in Ketambe.
(j) Hand-assisted bipedal scramble was the most common form of bipedalism in Sabangau.
(k) Pronograde Bridge has been identified as an important strategy for movement on the smallest supports (Thorpe et al., 2009).

locomotion, particularly orthograde suspension, dominates orangutan locomotor behavior in all forest types (Thorpe and Crompton, 2005, 2006; chapter 2). In Sabangau, suspensory locomotion took place on a wide range of supports, although tree trunks clearly played an important role, as they were involved in over 60% of suspensory locomotion (Figure 3.6e). In contrast, in dry-lowland forest in Sumatra, suspensory locomotion was predominantly associated with lianas, which accounted for over 60% of orthograde suspensory locomotion (Thorpe and Crompton, 2005). This further indicates that the closely spaced trunks in Sabangau fulfil a functional role provided by lianas in dry-lowland forest.

Compressive locomotion was associated with single support of the largest size category in both forest types. We would expect orangutans to walk quadrupedally on large, stiff supports (Figure 3.6g) wherever possible as this is likely to both increase safety and reduce the energetic cost of locomotion (Rosenberger and Strier, 1989; Strier, 1991; Warren and Crompton, 1998). Interestingly, compressive locomotion was associated with single tree trunks in Sabangau. This reflects the fact that orangutans travel lower in the canopy in disturbed peat-swamp and were often observed to walk quadrupedally on fallen tree trunks. Whilst tree falls are a natural phenomenon of forest dynamics, the manner in which peat-swamps are logged, via the creation of canals on which to float timber out of the forest, drains the peat, thereby reducing stability and increasing the incidence of tree falls (D'Arcy and Page, 2002). However, in contrast with orangutans in Sumatran dry-forest, orangutans in Sabangau often exibited compressive locomotion on multiple branches/boughs of the smallest size category. The use of small compliant supports has been shown to increase

the energetic cost of locomotion in both monkeys and lemurs (Alexander, 1991; Demes et al., 1995). However, orangutans have been found to employ unique strategies when negotiating small supports, such as long contact times and irregular gait to avoid the risk of resonance in branch sway (Thorpe et al., 2009). This is especially important in logged forests, typically dominated by small trees, and hence small branches. By distributing their body mass over multiple small supports, orangutans are able to increase stability, which is a vital strategy in traversing the canopy of disturbed forest (Figure 3.6h, j and k).

Our prediction (number 2) that orangutans in disturbed peat-swamp will exhibit greater mass-related variation in locomotion and support use as a result of the limited abundance of large branches was not entirely upheld in this study. The best-fitting models were produced when adult or flanged males were combined with the much smaller adult females, and subadult or unflanged males were combined with adolescents. This would indicate that factors other than body mass alone influence orangutan locomotion. Subadult males and adolescents used single small supports more than adult males and females indicating that both adolescents and subadult males employ more "risky" behaviour, and this has been observed during both play and fleeing from dominant flanged males (Thorpe and Crompton, 2006; per obs.). Juvenile orangutans were found to have a higher proportion of total hindlimb muscle mass compared to adult male orangutans (Payne et al., 2006ca, b) which has been attributed to the necessity for a more secure pedal grip as they exhibit fast and risky locomotion suggesting orangutans become more cautious as they become larger and older ((Thorpe and Crompton, 2006). In addition, adult males may simply be too heavy to use

the smallest supports unless their body mass is distributed over several supports, whereas adult females are perhaps more cautious in their selection of supports. This result supports the suggestion that experience with raising offspring causes adult females to be more conservative than other age-sex categories in their locomotion, and to select larger supports (Thorpe and Crompton, 2005; Thorpe et al., 2009). In addition, adult females in Sabangau selected larger trees for travel than other age-sex classes (chapter 4), adding further support to this hypothesis.

In contrast to our predictions based on the stunted structure of Sabangau (prediction 3), height in the canopy did have a strong association with support characteristics during locomotion. Height in the canopy had a direct influence on both the type and size of supports used during locomotion. When travelling above 10 m orangutans tended to use either single branches and boughs of the largest size category, or distributed their weight over multiple small supports. However, when travelling below 10 m, orangutans tended to used either single or multiple tree trunks, which provide the most continuous pathway for travel at lower levels. The mean bole height was 10.5 m in Sabangau (Table 3.4), suggesting that support availability above and below 10 m influences support selection, with trunks being the most prevalent support below 10 m.

3.5 Conclusions

Our results found that in contrast to Sumatran orangutans in dry lowland forest (Thorpe and Crompton, 2005), support type and support diameter (incorporating the number of supports used) did not have the strongest association with locomotor repertoire. The results of this study revealed a

number of differences in locomotion and support use between Sumatran orangutans (*P. abelii*) and the Bornean subspecies *P. p. wurmbii*. Where lianas played an important role in Sumatran dry lowland forest, in Sabangau the smaller girthed trunks played an important role during climbing and tree-sway as well as suspensory locomotion in Sabangau. This is particularly interesting as orangutans in both disturbed peat-swamp forest and dry lowland forest were found to have similar profiles in terms of preferred supports, the most notable exception being the preference for lianas in Sumatran dry forest (chapter 4). The way in which orangutans use tree trunks in disturbed peat-swamp forest, for tree sway, climbing and orthograde suspensory locomotion, suggests that the small trunks typical of this habitat fulfil a functional role provided by lianas in more pristine habitat.

Body mass was found to have a limited influence on orangutan locomotion, although the results of this study do suggest that adult males are too heavy for locomotion on single small supports. However, the results of this study support previous suggestions regarding the propensity of adult females towards more conservative locomotor behavior. Height had a strong association with support characteristics, indicating that orangutans in disturbed peat-swamp exploit the closely spaced trunks when travelling lower in the canopy, which provide the most continuous stratum for travel in many areas of this forest, although this appears to reflect support availability in the different strata. The classification of variables in this study are a result of the vast differences in habitat between the two sites, with support categories in the Sabangau reflecting a more stunted forest, with a lower canopy and smaller support sizes compared to Ketambe's more

heterogeneous forest structure which has a wider range of available supports.

CHAPTER 4

Forest Structure and Support Availability Influence Orangutan Locomotion in Borneo and Sumatra

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KLM developed the methods, collected and analysed the data and wrote the manuscript, MEH contributed to the writing of the manuscript, SKST assisted in the development of the methods and the writing of the manuscript

ABSTRACT

The influence of habitat structure and support availability on support use are important aspects of understanding locomotor behaviour in arboreal primates. We compared habitat structure and support availability in three orangutan study sites – two on Sumatra (*Pongo abelii*) in the dry-lowland forest of Ketambe and peat-swamp forest of Suaq Balimbing, and one on Borneo (*Pongo pygmaeus wurmbii*) in the disturbed peat-swamp forest of Sabangau – to better understand orangutan habitat use. Our analysis revealed vast differences in tree and liana density between the three sites. Sabangau had a much higher overall tree density, although both Sumatran sites had a higher density of larger trees. The two peat-swamp forests were more similar to each other than to Ketambe, particularly with regard to support availability. Ketambe had a wider variety of supports of different sizes and types, and a higher density of larger lianas than the two peat-swamps. Orangutans in all three sites did not differ substantially in terms of their preferred supports, although Sumatran orangutans had a strong tendency to use lianas, not observed in Sabangau. Differences in observed frequencies of locomotor behaviour suggest the homogeneous structure of Sabangau limits the locomotor repertoire of orangutans, with high frequencies of fewer behaviours, whereas the wider range of supports in Ketambe appears to have facilitated a more varied locomotor repertoire. There were no differences among age-sex classes in the use of arboreal pathways in Suaq Balimbing, where orangutans selected larger trees than were typically available. This was less apparent in Sabangau, where orangutans generally used trees in relation to their environmental abundance, reflecting the homogeneous nature of disturbed peat-swamp forest. These results demonstrate that forest architecture has an important influence on orangutan locomotion, which may become increasingly important as the structure of orangutan habitat continues to be altered

through human disturbance.

4.1 Introduction

CANT (1992) identified four key habitat-related problems that arboreal primates must deal with to resolve energetic challenges associated with arboreal locomotion: straightening the path of movement, negotiating large supports, crossing gaps between trees, and increasing speed along the path of movement. Gross canopy structure and the types and diameters of supports available for weight bearing have considerable influence on the possible solutions primates can employ to resolve these problems. A number of studies have demonstrated that the characteristics (e.g. type and diameter) of the supports used for weight bearing have substantial influence on the expressed locomotor repertoire of arboreal primates (e.g. Cartmill, 1985a; Cant, 1987b; Hunt, 1992; McGraw, 1996; Thorpe and Crompton, 2005). However, our understanding of the influence of habitat structure, and support availability vs. support use, on primate locomotion remains remarkably underdeveloped (McGraw, 1996; Warren, 1997; Dagosto and Yamashita, 1998; Youlatos et al., 2008), especially given its importance in avoiding erroneous inferences about species differences in locomotion that may actually result from animals inhabiting structurally different environments (e.g. Cant, 1992; Thorpe and Crompton, 2009). Previous studies of the positional behaviour of orangutans (*Pongo* spp.) imply that, whilst the types of orangutan arboreal locomotion employed do not differ substantially between species (beyond greater arboreality in Sumatran orangutans – *P. abelii* – that probably relates to the presence of a large, ground-dwelling predator, Cant, 1987b), the relative frequencies of positional behaviours do differ, with higher levels of pronograde (horizontal

trunk) and compressive locomotion, and lower levels of suspensory locomotion and tree-sway in Sumatra compared to *P. pygmaeus* in Borneo (Thorpe and Crompton, 2006, 2009; chapter 2). These differences are probably related to habitat structure (chapter 3) since Sumatran orangutans exhibited distinct patterns of association between the type, diameter and number of supports used and locomotion (Thorpe and Crompton, 2005; Thorpe et al., 2009); whereas, in Borneo, primary activity type (feeding or travelling) had the strongest influence on locomotion, and support type and diameter were most strongly associated with the height of the animal in the canopy and the age-sex class of the individual, respectively (chapter 3). In chapter 3, we proposed that these associations indicate the varied habitat structure of the dry lowland forest study site in Sumatra allowed Sumatran orangutans to use preferred locomotion/support combinations, whereas the homogeneous nature of the Bornean site studied (logged peat-swamp forest) led to Bornean orangutans being forced to use those supports that were most prevalent in the environment. Orangutans inhabit a number of different forest types, including dry lowland and hill dipterocarp forest, peat-swamp forest, freshwater-swamp forest, alluvial forest and heath (*kerangas*) forest (Rodman and Mitani, 1987; Knott, 1998; Morrogh-Bernard et al., 2003; Husson et al., 2009). These forest types differ substantially in terms of tree species composition, productivity and structure, and between the same habitats on Sumatra and Borneo. Primary productivity is likely to be substantially lower in Borneo than in Sumatran forests because of the latter's younger, more fertile volcanic soils (Wich et al., 2011; Marshall et al., 2009). Mixed-dipterocarp forests are generally tall forests, with the top of the canopy typically reaching 45 m (Whitmore, 1984). Alluvial forests are also species rich but have a lower canopy than dipterocarp forests (Proctor

et al., 1983). Undisturbed lowland peat-swamp forests have lower tree species richness and a generally medium (35-40 m) to low (15-25 m) closed-canopy layer. Mixed peat-swamp forest, such as that found in the orangutan research area in Sabangau, has a closed canopy layer between 15-25 m (Page et al., 1999). Freshwater-swamp forests have a varied structure which can range from low scrub with trees 10 m in height, to a structure similar to mixed lowland forest (MacKinnon et al., 1996). Heath (or *kerangas*) forests are found on white sand soils that are nutrient poor, highly acidic and free draining, and are frequently covered in a superficial peat layer. Although the most productive heath forests can resemble lowland-dipterocarp forests, heath forest structure generally tends to be characterized by shorter, smaller trees with a low single-layered canopy and heath forests share numerous features with peat-swamp forest including a large degree of species overlap (MacKinnon et al., 1996). The level of past and contemporary human disturbance also has an important impact on forest structure, since logging often results in large gaps in the continuous upper-canopy layer, which in turn increases the quantity of vegetation in the lower canopy, resulting in a more rugose and discontinuous forest canopy (Vogel et al., 2009). To date, detailed studies of positional behaviour have only been conducted on orangutans inhabiting dry lowland forest (Ketambe, Sumatra; Thorpe and Crompton, 2005, 2006, 2009; Thorpe et al., 2007aa, b, 2009) and mixed peat-swamp forest (Sabangau, Borneo; chapter 2; chapter 3).

Lianas are woody vines that are flexible in compression, yet strong in tension, and are an important structural component of tropical forests, typically constituting around 25% of the woody stem density and species

diversity (Gentry, 1991; Appanah et al., 1992). In addition, lianas have an essential role in many aspects of forest dynamics, including suppressing tree regeneration, increasing tree mortality, providing an important food source for forest fauna and, crucially, providing pathways for arboreal animals that link trees together (Grand, 1984; Emmons and Gentry, 1983). It has been noted that there is a difference in orangutan liana use both within Borneo, and between Borneo and Sumatra (Cant, 1987b; Thorpe and Crompton, 2009; chapter 3). Cant (1987b) found a higher proportion of liana by *P. pygmaeus morio* at Mentoko, Borneo, compared to subsequent studies in other forests, and also describes "curtains of lianas" in the forest. Use of lianas by orangutans in mixed dry-forest in Sumatra was also found to be high, especially when entering emergent feeding trees (Thorpe and Crompton, 2005); whereas in chapter 3 we observed a very low frequency of liana use in Sabangau, Borneo. Peat-swamp forests are likely to have lower densities of lianas than mixed dry-forests, as liana density is associated with nutrient availability and peat soils contain lower available nutrients (Whitten et al., 2000).

To understand the effect of habitat variation on orangutan locomotion, we quantified forest structure and support availability at the two study sites for which orangutan locomotion and support use are well documented: Sabangau (disturbed peat-swamp forest, Central Kalimantan, Borneo, *P. pygmaeus wurmbii*) and Ketambe (dry lowland forest, Leuser Ecosystem, Sumatra, *P. abelii*) (Thorpe and Crompton, 2005, 2006, 2009; Thorpe et al., 2007a, b, 2009; chapter 2). We also obtained new locomotor and habitat data for orangutans at Suaq Balimbing, an undisturbed peat-swamp forest in the Leuser Ecosystem, Sumatra (van Schaik, 1999). This allowed for comparison

of the relationship between habitat structure and locomotion within a single species (*P. abelii*), and comparison of differences within a single habitat type (peat-swamp forest) between species, helping us to tease apart the relative influence of species vs. habitat on orangutan locomotion.

Within each study site, we also investigated whether support use mirrored support availability or whether supports were selected because of properties that made them preferable for locomotion. In light of previous primate studies of orangutan locomotor behaviour (e.g. Thorpe and Crompton, 2005, 2009; Thorpe et al., 2009; chapter 2, chapter 3), we hypothesize that 1) orangutans in Sumatra (Ketambe and Suaq Balimbing) will show stronger preference/avoidance strategies given the more heterogeneous nature of the forest, whereas 2) orangutans in disturbed peat-swamp forest (Sabangau), which is likely to be more homogeneous, will be less selective over their substrate use.

Orangutans are well known for their use of arboreal pathways (MacKinnon, 1974; Cant, 1992; Thorpe and Crompton, 2005), which might explain the limited influence of age-sex class on locomotor behaviour (Thorpe and Crompton, 2005). However, how travel routes are selected and whether these strategies differ between species or as a consequence of habitat variation is largely unknown. Numerous features of the canopy could potentially influence the selection of travel routes; for example, the connectivity of tree crowns will affect the size and type of gaps between trees, which would be expected to influence how an orangutan might traverse these gaps. To investigate this, we compared the structural features of trees used during travel in Suaq Balimbing and Sabangau, in order to

understand inter-site differences between the two peat-swamp study sites and intra-site differences between age-sex classes. Given the use of arboreal pathways by orangutans we further hypothesize that there will be: 3) little variation in travel trees used between the age-sex classes; 4) differences in arboreal pathways between Suaq Balimbing and Sabangau, as a result of differences in forest structure between the sites; 5) less variation in travel trees used in Sabangau compared to availability in the environment, given the apparently more homogeneous nature of this forest; whereas 6) in Suaq Balimbing orangutans will select for trees that have attributes that are likely to reduce vertical displacement (e.g. greater connectivity between crowns), given the seemingly more open and discontinuous canopy.

4.2 Methods

Study Sites

Research took place in three study sites, two of which are located in Sumatra and one on Borneo. Ketambe is situated in the northeast of the Leuser Ecosystem, Sumatra (3° 41′ N, 97° 39′ E), and mainly comprises primary mixed dry-lowland rainforest. Forest structure was quantified during the period May 2010 to July 2010. Suaq Balimbing is situated in the western coastal plain of the Leuser Ecosystem, Sumatra (3° 42′ N, 97° 26′ E). The site mainly comprises peat-swamp forest, in which the peat layer increases in thickness with increasing distance away from the river (Wich et al., 2009). All data were obtained here during the period August 2010 to April 2011, and whilst the behavioural study at Ketambe was undertaken some years earlier, since this particular area has not been subjected to logging or fire, it is thought that the overall structure will not vastly differ from when the

study was undertaken. The Natural Laboratory for the Study of Peat-Swamp Forest research station, in Sabangau, southern Borneo (2° 03′ S, 113° 54′ E) is also peat-swamp forest. The study site was selectively logged under concession from 1966 to 1996, and then illegally logged from 1996-2004. Data collection for this study was undertaken between March 2007 and September 2007, and April 2009 and January 2010. An overview of the three study sites is provided in Table 4.1.

Habitat Survey

To characterise forest structure, twenty 100 m-long transects were established in each of the sites. The location and orientation of each transect was randomly selected within the orangutan study grid at each site, was sufficiently far apart ($\geq$ 25 m) to ensure that trees were never sampled twice, and was oriented so that no two transects intersected. Sample points were taken at 25 m intervals along each transect (5 points per transect) using the point-center-quarter method (PCQM, Cottam and Curtis, 1956), which has been widely used in previous primate studies (e.g. Cannon and Leighton, 1994; Villard et al., 1995; Marsh and Loiselle, 2003; Balko and Underwood, 2005; Teelen, 2007). The distance to the nearest tree from the point centre (DTPC) was measured in each quadrant, as defined by the transect direction and its perpendicular. Within each quadrant, the diameter at breast height (DBH, 1.3 m above the ground) of the nearest tree for each of the diameter classes was measured, allowing quantification of tree density for each size class.

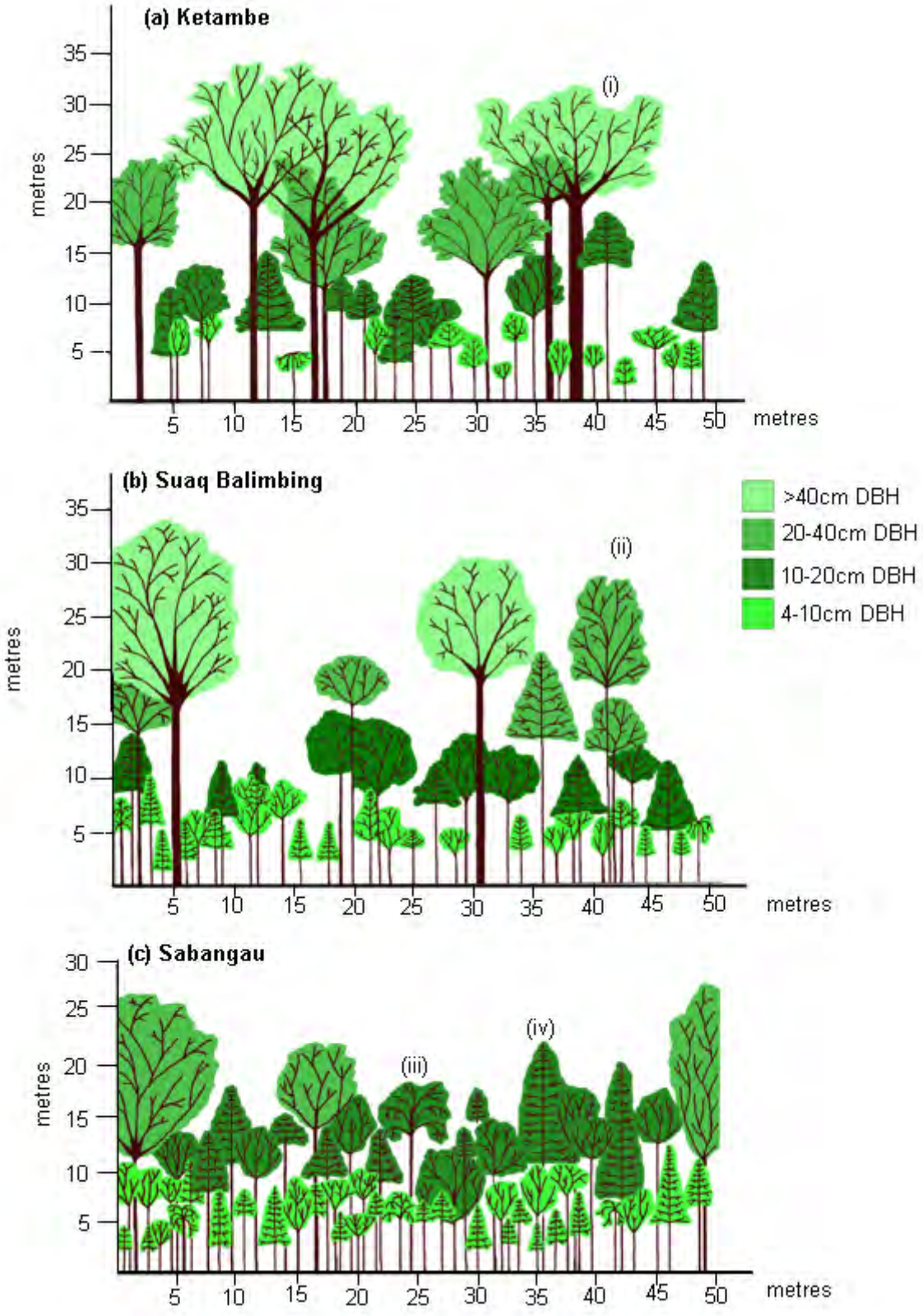
To quantify support availability, 40 points were randomly selected from the 100 points along the PCQM transects. In each quadrat, for the nearest tree

Table 4.1 – Overview of Study Sites

	Sabangau	Suaq Balimbing	Ketambe
Location	Central Kalimantan, Borneo	Gunung Leuser, Aceh, Sumatra	Gunung Leuser, Aceh, Sumatra
Species	*Pongo pygmaeus wurmbii*	*Pongo abelii*	*Pongo abelii*
Orangutan Standardised Density[a]	2.35 ind/km^2	7.44 ind/km^2	3.24 ind/km^2
Forest Type	Peat-Swamp Forest	Peat-Swamp Forest	Dry Lowland Forest
Canopy Height[b,c]	15-25 m	15-25 m	35-40 m
Disturbance	Logged	Unlogged	Unlogged
Productivity	Low	High	High
Rainfall[d]	2,790 mm	3,400 mm	3,288 mm
Mean Elevation[a,d]	10 masl	10 masl	320 masl upwards

[a] Husson et al. (2009)
[b] Page et al. (1999)
[c] Whitmore (1984)
[d] Wich et al. (2009)

Figure 4.1 – Approximate Representation of the Forest Profile in the Three Sites



Profiles are based on distances and densities obtained from a randomly selected transect at each site using the PCQM (Mueller-Dombois and Ellenberg, 1974), together with actual measurements of structural attributed (e.g. tree height, bole height, crown diameter, crown shape, crown connectivity). (i) wide cone; (ii) narrow cone; (iii) umbrella; (iv) monopodial (after Cant et al. 2001, 2003).

≥10 cm DBH and ≥4 cm DBH (n = 160 trees at each site for each size class), we measured DTPC and DBH, plus tree height and bole height (height to the first main bough) using a clinometer. For these trees we also measured crown diameter using a tape measure along the ground; crown shape (narrow cone, wide cone, umbrella, monopodial; Figure 4.1); crown connectivity (a 4-point scale was used to indicate the position of the crown relative to neighbouring crowns both on the vertical and horizontal, in terms of contact with or proportion overlapping neighbouring crowns: 1 = 0-25%, 2 = 26-50%; 3 = 51-75%; 4 = 76-100%, after Whitten, 1982); and crown volume, calculated using crown height and diameter incorporating correction factors specific to the crown shape (monopodial = 0.1964; narrow cone = 0.2619; wide cone = 0.2945; umbrella = 0.4909;Coder, 2000). Support availability was quantified by counting the number of boughs and branches for all classes >2 cm diameter within the crown. Boughs were defined as those connected to the trunk of the tree, branches were defined as those connected to either boughs or other branches. The number of smaller branches (≤2 cm diameter) was difficult to count accurately and therefore a semi-logarithmic scale was used to estimate the number of these supports (Table 4.2). The number and size of lianas present in each tree crown were counted precisely. Forest profile diagrams presented in Figure 4.1 provide an impression of the overall structure of each of the sites used in this study.

Support Use

Orangutan positional behaviour observations in Ketambe were made by a single observer (SKT), and all observations in Suaq Balimbing and Sabangau were made by a single observer (KLM) during nest-to-nest follows of wild orangutans, following the same methods. Instantaneous samples on the

Table 4.2 – Scale Used for the Estimation of the number of branches (≤2 cm diameter)

Number of Branches[a]	Mid-value used in Calulations
1-5	3
6-10	8
11-25	18
26-50	38
51-100	75
101-500	300
501-1,000	750
1,001-2,000	1,500
2,001-4,000	3,000
4,001-6,000	5,000
6,001-8,000	7,000
8,001-10,000	9,000

[a] Scale established by Morrogh-Bernard (2009) for long-term phenological monitoring in the Sabangau.

1-min mark were used to obtain detailed data of support use during locomotion in nest-to-nest follows of wild orangutans. Data collected at each sample point included the support type (branch, bough, trunk, liana); support diameter (<4 cm; 4-10 cm, 10-20 cm, >20 cm) and the number of weight-bearing supports (1, 2, 3, 4, >4). These methods have been described in detail elsewhere (Thorpe and Crompton, 2005; chapter 2, chapter 3). For observations of support use during locomotion; 1,762 observations were obtained from orangutans in Suaq Balimbing (this study) and 2,037 in Sabangau (chapter 2, chapter 3); and 1,783 in Ketambe (Thorpe and Crompton, 2005).

Travel Trees

During nest-to-nest follows of wild orangutans in Suaq Balimbing and Sabangau, the trees in which focal animals travelled were marked with

ribbon and their GPS positions taken, in order that they could be returned to at a later date. These trees were then re-located and the same measurements taken as described in the previous section for the random sample. In addition, we measured the trunk-to-trunk distance and the gap distance or degree of crown overlap (measured as projected to the ground, using a tape measure in the direction of travel to the next tree). Unfortunately it was not possible to obtain these data for Ketambe, as the locomotor study was carried out a number of years earlier than the current work (Thorpe and Crompton, 2005). These variables were compared between age-sex classes (flanged males, sexually active females, non-sexually active females and unflanged males, as defined by Morrogh-Bernard et al., 2009) to see if there were any differences in the structural features of trees used during locomotion; between the trees used for locomotion and those from the random sample (i.e., support use vs. environmental availability); and between sites.

Statistical Analysis

A t-test or one-way ANOVA (with Tukey post hoc) was used where data did not violate assumptions of normality and heterogeneity of variance; otherwise variables were compared using Kruskal-Wallis non-parametric test and the Mann-Whitney U-test *post hoc*. Given the need for multiple comparisons in the Mann-Whitney U-test, the significance level was lowered according to Bonferroni probabilities (dividing the Type I error rate, e.g. 0.05, by the number of comparisons; Field, 2005). Categorical data were compared using Chi-squared tests.

Overall tree and liana density (number of stems/ha) was calculated by

dividing 1 by the square of the mean of all distances, measured in metres, and then multiplying by 10,000 to convert the figure from m^2 to ha^2 (Cottam and Curtis, 1956). Similarly, density was calculated for each sampling point and these values were used to compare the three sites. Vacant quarters were corrected for using correction factors detailed in Warde and Petranka (1981).

Jacobs' D value (Jacobs, 1974) was used as an index to assess preference for different main weight bearing supports across the three study sites. This index has been used in a number of primate studies both for canopy selection (e.g. Cannon and Leighton, 1994; Machairas et al., 2003) and for support preference (Warren, 1997; Youlatos, 2008; Youlatos et al., 2008). Although a variety of alternative electivity indices do exist, comparisons of these have found that, with the exception of Strauss' L, all the indices are broadly comparable and are useful measures of preference (Lechowicz, 1982).

Jacob's D is calculated as: Jacobs D = (r - p) / (r + p - 2rp)

where r is the relative use of the support and p is the relative availability for the support within the forest. This method standardizes the relationship between support use and support availability to between +1 and -1, where + 1 indicates maximum preference and -1 indicates maximum avoidance, and is symmetrical around 0, indicating neutrality of choice (i.e. use in direct relation to abundance).

4.3 Results

Tree and Liana Density

Ketambe, Suaq Balimbing and Sabangau were found to have significantly different tree densities (Table 4.3). Small trees dominated in all three forests, but Sabangau had a significantly higher density of trees <20 cm DBH compared to Ketambe and Suaq Balimbing, and Suaq Balimbing had a significantly higher density of these trees than did Ketambe (Table 4.3). In contrast, for medium sized trees (20-40 cm DBH), densities were similar in both peat-swamp forest sites, and significantly higher than in dry-forest. For larger trees (>40 cm DBH), however, densities were similar in the Sumatran sites (Ketambe and Suaq Balimbing), but significantly lower in the Borneo site (Sabangau). Suaq Balimbing had the highest density of small lianas (<2 cm diameter), whereas the density of small lianas was similar in Ketambe and Sabangau. The density of medium lianas (2-4 cm), densities was higher in Ketambe and Suaq Balimbing than in Sabangau. Finally, for large lianas (>4 cm) densities were significantly higher in Ketambe than in the two peat-swamp forest sites, where densities were similar (Table 4.3).

Canopy Variables and Support Availability

The mean DBH of trees >10 cm was significantly higher in Ketambe than in Suaq Balimbing and Sabangau, but similar between Suaq Balimbing and Sabangau (Table 4.4). Crown volume, crown width and tree height were also significantly higher in Ketambe than in Suaq Balimbing and Sabangau, but no significant difference was found between the two peat-swamp forest sites (Table 4.4). There was a significant difference between the three study sites in terms of crown connectivity ($\chi 2$=87.196; df=6; P$\leq$0.001, Figure 4.2), with

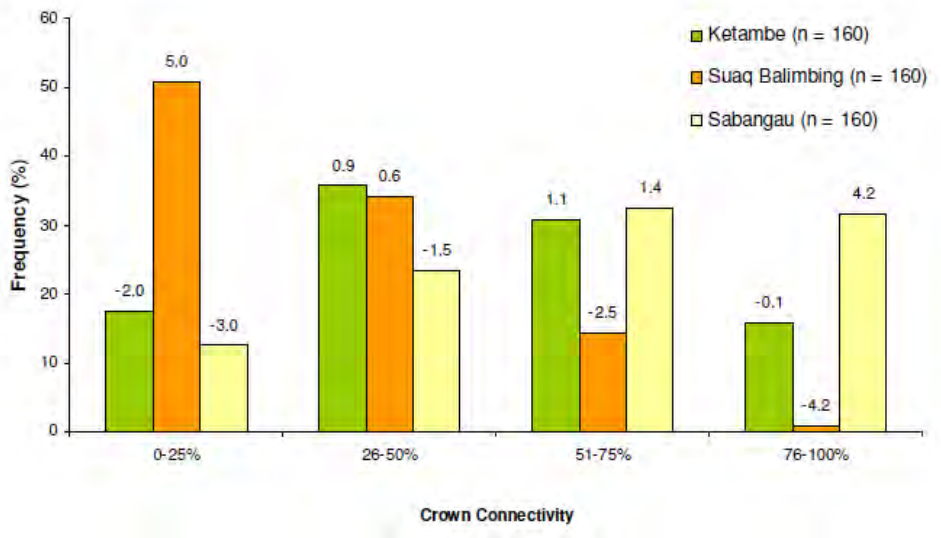
Table 4.3 – Comparison of Tree and Liana Densities in Three Study Sites

	Kruskal - Wallis	Stem Density			Mann-Whitney U-test (U) *post hoc*		
	(H)	Ketambe	Suaq	Sabangau	1	2	1
Variable	**1 vs 2 vs 3**	**(1)**	**(2)**	**(3)**	**vs 2**	**vs 3**	**vs 3**
Trees							
Density <4 cm DBH	118.165***	1,182	1,942	4,505	***	***	***
Density ≥4 - <10 cm DBH	130.056***	654	1,000	2,011	***	***	***
Density ≥10 - <20 cm DBH	101.874***	249	426	687	***	***	***
Density ≥20 - <40 cm DBH	25.328***	126	181	214	**	ns	***
Density ≥40 cm DBH	54.121***	67	59	17	ns	***	***
Lianas							
Density <2 cm DBH	38.351***	1,025	1,352	924	***	***	ns
Density ≥2 - <4 cm DBH	26.778***	202	177	141	ns	***	*
Density ≥4 cm DBH	23.387***	119	75	53	**	ns	***

Kruskal-Wallis test (DF = 2), Mann-Whitney U-test *post hoc* (DF = 1)
Kruskal-Wallis: *P≤0.05; **P≤0.01; ***P≤0.001

Mann-Whitney U-test (according to Bonferroni probabilities): *P≤0.017; **P≤0.0003; ***P≤0.00003

Figure 4.2 – Frequency Distribution of Crown Connectivity for Trees (>10 cm DBH) Across Three Study Sites



* *Figures are standardised cell residuals*

connectivity in Sabangau > Ketambe > Suaq Balimbing.

The forests at Ketambe, Suaq Balimbing and Sabangau also differed in terms of the number of different-sized supports in the forest canopy (Table 4.4). Ketambe had a significantly larger number of supports than the other two sites for the majority of support classes. Overall, the availability of supports at Suaq Balimbing and Sabangau were found to be relatively similar, although Suaq Balimbing had a significantly higher density of 4-10 cm and >10 cm branches, and <2 cm boughs (Table 4.4). There was a significantly higher number of lianas in Ketambe than in the two swamp forests, but no significant difference was found between Suaq Balimbing and Sabangau (Table 4.4).

Table 4.4 – Comparison of Canopy Variables and Supports for Trees >10 cm DBH across Three Study Sites

	Kruskal-Wallis	Mean			Mann-Whitney U-test (U) *post hoc*		
	(H)	Ketambe	Suaq	Sabangau	1	2	1
Variable	1 vs 2 vs 3	(1)	(2)	(3)	vs 2	vs 3	vs 3
		n = 160	n = 160	n = 160			
DBH	15.846***	29.69	20.54	17.40	*	ns	***
Crown Volume	27.472***	270.11	93.94	84.18	**	ns	**
Crown Width	36.907***	7.47	5.29	5.32	***	ns	***
Tree Height	18.414***	20.33	17.03	16.51	***	ns	***
Number of Lianas	24.791***	7.11	4.31	1.62	**	ns	***
Boughs							
<2 cm	13.456***	15.43	27.45	14.67	**	**	ns
2 - 4 cm	2.011^{ns}	10.22	7.97	9.45	ns	ns	ns
4 - 10 cm	19.212***	6.57	3.05	3.67	***	ns	**
>10 cm	41.830***	3.58	1.23	0.45	***	ns	***
Branches							
<2 cm	21.864***	1,600.29	1,046.44	892.06	***	ns	***
2 - 4 cm	12.125**	19.17	9.37	8.08	**	ns	**
4 - 10 cm	20.188***	4.70	1.92	1.80	**	*	***
>10 cm	28.375***	1.78	0.78	0.03	**	***	***

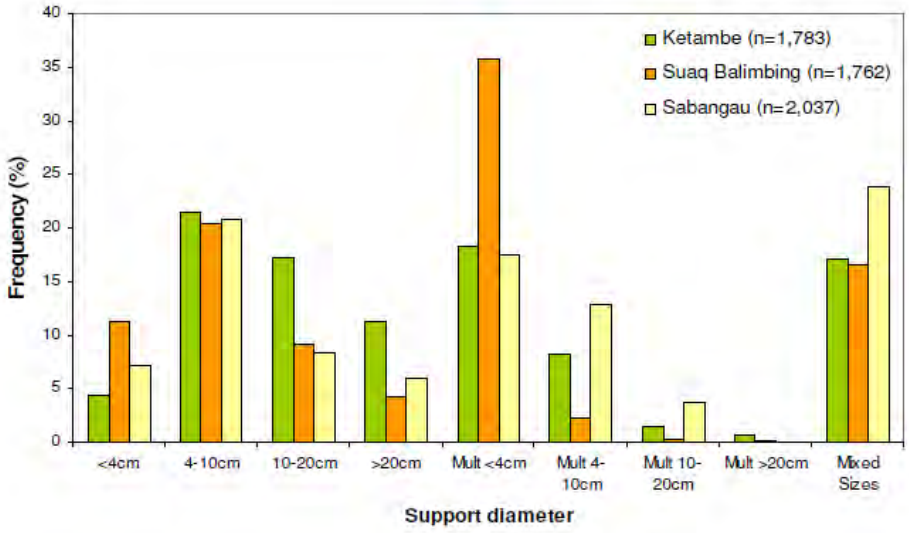
Kruskal-Wallis test (DF = 2), Mann-Whitney U-test post hoc (DF = 1)
Kruskal-Wallis: *P≤0.05; **P≤0.01; ***P≤0.001; ns = not significant

Mann-Whitney U-test (according to Bonferroni probabilities): *P≤0.017; **P≤0.0003; ***P≤0.00003; ns = not significant

Support Use

There were considerable differences in the size of supports used by orangutans between the three sites (χ2=616.72; df=16; P≤0.001; Figure 4.3). The most striking result was that orangutans in Suaq Balimbing used the multiple supports of the very smallest diameter (<4 cm) much more than was observed in both Ketambe and Sabangau. In Ketambe, orangutans used single larger supports (10-20 cm and >20 cm diameter) more than was observed in the two peat-swamp sites. Orangutans in all three study sites used single supports of 4-10 cm diameter with similar frequencies, although

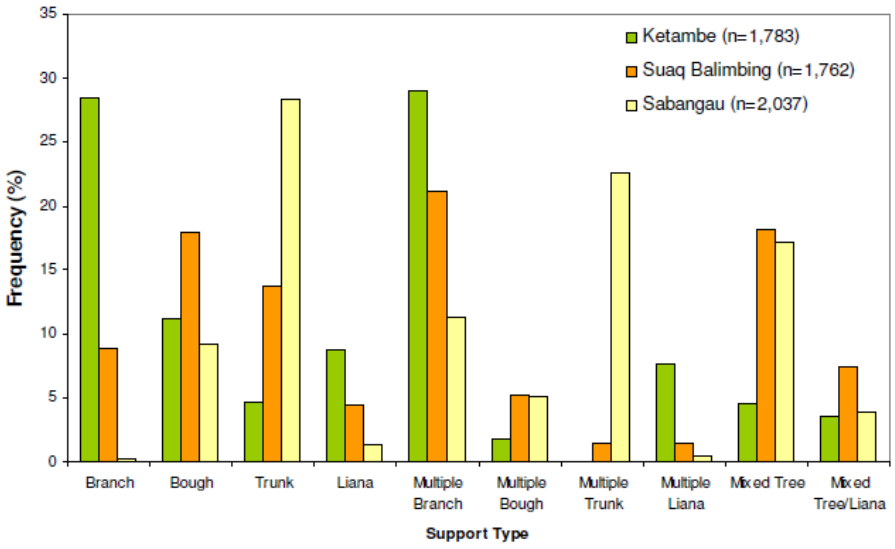
Figure 4.3 – Frequency Distribution for Support Diameter used by Orangutans During Locomotion Across Three Study Sites



orangutans in Sabangau used multiple supports of this size much more than was observed in the Sumatran sites. The Sabangau orangutans also employed multiple supports of 10-20 cm more often than elsewhere.

There was also a significant difference in the types of supports used between the three sites ($\chi 2=2495.49$; df=18; $P \leq 0.001$; Figure 4.4). The most notable differences were that orangutans in Ketambe used both single and multiple branches, and single and multiple lianas, more than observed at other sites, whereas orangutans in Sabangau used both single and multiple trunks more than observed in the two Sumatran forests. Orangutans in Suaq Balimbing used single boughs more than observed elsewhere. In peat-swamp forest, multiple boughs and mixed tree supports (i.e. any combination of trunk/branch/bough) were used more often than in more than in dry forest.

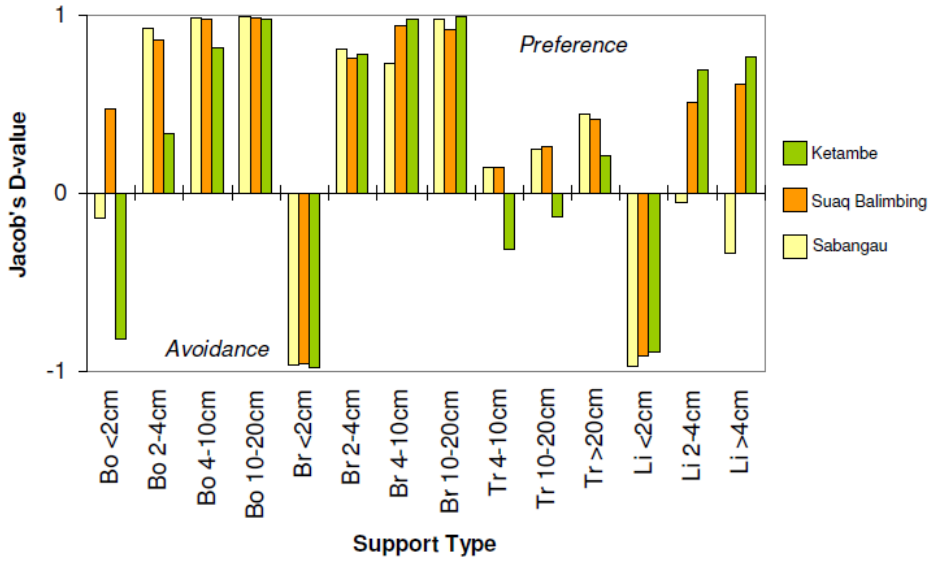
Figure 4.4 – Frequency Distribution for Support Type used by Orangutans During Locomotion Across Three Study Sites



Assessment of Preference

Orangutans at all three sites had broadly similar profiles of preferred supports (Figure 4.5), although some differences were apparent. While orangutans at all three sites showed strong avoidance of the smallest branches and lianas (<2 cm diameter), the pattern for the smallest boughs did not follow the same trend. Although orangutans in Ketambe showed strong avoidance for boughs of <2 cm diameter, in Sabangau they showed only slight avoidance whereas in Suaq Balimbing they showed a preference. Orangutans in both Suaq Balimbing and Sabangau used boughs 2-4 cm much more than was observed Ketambe. All orangutans used trunks <20 cm DBH in similar proportions to their availability in the environment, however, preference values were slightly positive in the two peat-swamp forests (Sabangau and Suaq Balimbing) but negative in dry-forest (Ketambe). In all three sites, orangutans showed a slight preference for trees

Figure 4.5 – Jacob's D-Value for Preference and Avoidance of Supports During Locomotion



>20 cm DBH. Orangutans in the two Sumatran sites showed a strong tendency for using lianas in the 2-4 cm and >4 cm diameter categories, whereas in the Bornean site orangutans used lianas 2-4 cm diameter in similar proportions to their availability and showed a slight avoidance of larger lianas >4 cm.

Travel Trees

Travel trees are trees which are used by orangutans for travel, they may rest in them but they differ from feeding trees in that orangutans were not observed feeding when in them. In Sabangau there was a significant difference in the trees used for travel between the age-sex classes in terms of DBH (ANOVA, F=12.368; df=3; $P \leq 0.001$), crown width (ANOVA, F=4.419; df=3; $P \leq 0.01$) and tree height (ANOVA, F=7.450; df=3; $P \leq 0.001$): sexually active females used larger trees than the other age-sex categories (Tukeys

post hoc, Table 4.5). There was also a significant difference among age-sex classes in the trunk-to-trunk distance between travel trees (ANOVA, F=6.859; df=3; P$\leq$0.001) in Sabangau, with the mean distance being the greatest for flanged males and the smallest for non-sexually active females. However, there was no significant difference in the degree of crown overlap or gap size. In Suaq Balimbing there were no significant differences in trees used for travel between the age-sex classes in any of the variables analyzed (Table 4.5).

The trees used by orangutans for travel in Suaq Balimbing differed significantly from the random sample of trees. "Travel trees" had a larger DBH, crown width and crown volume, and were taller than the random sample (Table 4.6). However, in Sabangau, travel trees did not differ significantly from the random sample in any variable measured, except for tree height, which was taller for travel trees (Table 4.6). There was also a marked difference in the number of supports found in travel trees in Suaq Balimbing, which had significantly more branches and boughs of all sizes, whereas in Sabangau the number of supports in the travel trees was similar to those obtained in the random sample (Table 4.7). In both sites the number of lianas in the crowns of travel trees was similar to the random sample with the exception of the smallest lianas in Suaq Balimbing (Table 4.7).

Comparison between the two peat-swamp forest sites revealed a larger DBH of trees used for travel in Suaq Balimbing than Sabangau (27.7cm vs 12.6cm; t=12.342; df=851; P$\leq$0.001), even though there was no significant difference in the mean DBH of the random samples between the two sites (12.8cm vs 11.4cm; t=1.226; df=318, P=0.221; trees >4cm DBH); plus a greater

Table 4.5 – One-Way Analysis of Variance and Means Separation Tests for "Travel Trees" by Age-sex Class in Peat-swamp Forest

				Age-Sex Class[a] (Means)				Tukey's Test *post hoc*[b]					
				FM	SAF	UFM	NSAF	1	1	1	2	2	3
Variable	**F**	**df**	**P**	**(1)**	**(2)**	**(3)**	**(4)**	**vs 2**	**vs 3**	**vs 4**	**vs 3**	**vs 4**	**vs 4**
Suaq Balimbing				**(n = 78)**	**(n = 190)**	**(n = 157)**	**(n = 119)**						
DBH (cm)	0.622	3	0.601	30.60	26.80	27.50	28.70	ns	ns	ns	ns	ns	ns
Height (m)	1.413	3	0.238	16.80	16.40	15.90	17.40	ns	ns	ns	ns	ns	ns
Crown Width (m)	6.747	3	0.429	5.59	5.36	5.38	5.84	ns	ns	ns	ns	ns	ns
Trunk-to-trunk Distance (m)	0.438	3	0.726	4.49	4.13	4.00	4.28	ns	ns	ns	ns	ns	ns
Gap Size (m)	1.389	3	0.246	2.36	2.19	2.22	2.59	ns	ns	ns	ns	ns	ns
Crown Overlap (m)	0.014	3	0.998	1.47	1.45	1.45	1.41	ns	ns	ns	ns	ns	ns
Sabangau				**(n = 46)**	**(n = 61)**	**(n = 89)**	**(n = 122)**						
DBH (cm)	12.368	3	0.000	11.60	15.60	13.10	10.90	***	ns	ns	*	***	*
Height (m)	7.450	3	0.000	12.40	15.70	13.95	13.10	***	ns	ns	*	***	ns
Crown Width (m)	4.419	3	0.005	3.53	4.48	4.00	3.94	**	ns	ns	ns	ns	ns
Trunk-to-trunk Distance (m)	6.859	3	0.000	3.89	3.29	2.80	2.57	ns	*	***	ns	ns	ns
Gap Size (m)	2.231	3	0.095	1.60	1.19	0.96	0.99	ns	ns	ns	ns	ns	ns
Crown Overlap (m)	1.687	3	0.172	0.62	1.41	1.21	1.45	ns	ns	ns	ns	ns	ns

[a] FM = flanged male; SAF = sexually active female; UFM = unflanged male; NSAF = non-sexually active female

[b] Tukey's Test post hoc: *P≤0.05; **P≤0.01; ***P≤0.001; ns = not significant

Table 4.6 – Comparison of Attributes of Travel Trees and a Random Sample in Two Peat-swamp Forests

		Mean				
Site	**Variable**	**Used**	**Random[a]**	**t**	**df**	**Significance**
Suaq		**(n = 544)**	**(n = 160)**			
	DBH (cm)	27.90	12.80	8.636	702	***
	Crown Width (m)	5.90	4.30	6.590	702	***
	Height (m)	18.10	11.70	10.818	702	***
	Crown Volume	104.95	44.04	3.115	702	**
Sabangau		**(n = 308)**	**(n = 160)**			
	DBH	12.70	11.40	1.912	476	ns
	Crown Width (m)	4.00	4.30	0.908	476	ns
	Height (m)	13.60	11.90	0.180	476	***
	Crown Volume	36.50	49.90	1.196	476	ns

mean height of trees used (16.4m vs 13.7m; t=6.827; df=824; P$\leq$0.001) and greater crown width in Suaq Balimbing (5.5m vs 4m; t=9.124; df=848, P$\leq$0.001). The trunk-to-trunk distance between consecutive travel trees was also larger in Suaq Balimbing than Sabangau (4.2m vs 2.9m; t=7.5; df=746; P$\leq$0.001), as was the degree of crown overlap (2.31m vs 1.33m; t=7.350; df=540; P$\leq$0.001). There was no difference in the mean gap size between the two sites (1.4m vs 1.2; t=1.500; df=176; P=0.118).

Locomotion

Torso-orthograde suspensory locomotion, particularly orthograde clamber, dominated orangutan locomotion in all three study sites (Table 4.8), although it was most frequently observed in Sabangau. Torso-pronograde

Table 4.7 – Comparison of Support Attributes between Travel Trees and a Random Sample[a]

	Suaq[b]				Sabangau[c]			
	Mean				Mean			
Variable	Travel Trees	Random	t	P	Travel Trees	Random	t	P
Boughs								
<2 cm	11.0	14.5	3.899	***	13.9	12.3	1.819	ns
2-4 cm	4.6	2.5	3.454	***	5.4	2.5	6.090	***
4-10 cm	2.9	0.8	6.824	***	0.9	0.8	0.538	ns
>10 cm	1.4	0.2	5.012	***	0.1	0.3	1.915	ns
Branches								
<2 cm (median)	841.4	488.3	5.106	***	852.5	718.6	1.690	ns
2-4 cm	15.0	3.4	2.094	*	2.6	2.3	0.580	ns
4-10 cm	3.8	0.7	2.526	*	0.3	0.6	1.458	ns
>10 cm	0.9	0.2	2.015	*	0.01	0.01	0.427	ns
Lianas								
<2 cm	3.6	2.7	1.978	*	1.0	0.7	1.850	ns
2-4 cm	0.3	0.3	0.900	ns	0.3	0.2	0.907	ns
>4 cm	0.1	0.1	0.719	ns	0.01	0.04	1.942	ns

t-test: *P≤0.05; **P≤0.01; ***P≤0.001
[a] Random sample based on the nearest tree >4 cm DBH using the PCQM
[b] Suaq: Travel Trees: n = 544; Random Sample: n = 160 (df = 702)
[c] Sabangau: Travel Trees: n = 290; Random Sample: n = 160 (df = 448)

suspension and bipedalism were more common in the two Sumatran sites than in Borneo. Tree-sway was more commonly observed in peat-swamp, whereas bridge was slightly more common in dry lowland forest. Quadrupedalism was observed at a higher frequency in dry lowland forest than in the two peat-swamp sites, although frequencies were similarly divided between symmetrical gait walk and pronograde scramble in each of the sites. Climbing was slightly higher in the Sumatran sites than it was in Sabangau, and vertical scramble occurred much more often in Ketambe than in either peat-swamp site. For a full list of locomotor behaviour across the

three study sites see (Appendix B)

4.4 Discussion

We quantified the structural features of the arboreal environment that were likely to impact on orangutan locomotor behaviour. As expected, significant variations in habitat structure and the availability of supports were discovered between sites, which is reflected in observed differences in orangutan support use in different habitat types, and differences in the trees used during travel between the two peat-swamp sites. Interestingly, however, we also found that orangutans across the three distinctly different study sites had an essentially similar profile of preferred supports.

Sabangau had a much larger total tree density than was found in either Suaq Balimbing or Ketambe, yet, as a likely consequence of past disturbance and low peat nutrient levels in Sabangau, had only a low density of large trees (>40 cm DBH). In terms of tree density, Ketambe and Sabangau were at two opposite extremes of a gradient, with Suaq Balimbing lying between the two. Suaq Balimbing and Sabangau were found to have a similar density of medium sized trees (20-40 cm); whereas for the largest trees (>40 cm DBH) Suaq Balimbing and Ketambe were more similar. Mean tree DBH was significantly higher in Ketambe than in Suaq Balimbing, however, indicating that the "largest trees" are smaller in Suaq Balimbing.

We anticipated that Sabangau would have the highest density of small lianas because of past disturbance; however, Sabangau and Ketambe were found to have a similar density of small lianas (<2 cm DBH) whereas Suaq Balimbing had the highest density of small lianas. Suaq Balimbing and

Table 4.8 – Percentages of Commonly Observed Locomotor Modes in Three Orangutan Study Sites

Mode	Submode	Ketambe[a]	Suaq Balimbing	Sabangau
Quadrupedal and Tripedal Walk		17.6	10.8	8.5
	Walk	8.0	5.2	4.2
	Pronograde Scramble	9.4	5.6	4.3
Torso-orthograde Locomotion		35.0	40.4	47.9
	Brachiation	6.2	7.6	4.0
	Forelimb Swing	8.4	6.2	2.9
	Orthograde Clamber	14.4	21.3	35.9
	Orthograde Transfer	6.1	4.8	5.0
Torso-pronograde Suspension		3.6	3.4	1.3
	Inverted Pronograde Walk	2.3	2.8	0.4
	Inverted Pronograde Scramble	1.3	0.6	0.7
Forelimb-hindlimb Swing		0.3	2.0	1.0
Bipedal Walk		7.3	5.4	3.2
	Bipedal Walk	1.6	0.6	0.1
	Assisted Bipedal Walk	5.6	4.8	3.2
Bridge		2.8	1.9	1.9
Vertical Climb		16.0	13.3	9.8
	Flexed-elbow	5.6	9.0	6.4
	Extended-elbow	1.2	0.5	0.8
	Vertical Scramble	7.1	2.0	0.8
Vertical Descent		9.4	6.6	5.2
Drop		1.8	0.8	1.1
Ride		0.5	0.6	0.8
Sway		5.6	14.9	19.0

[a] Data from Thorpe and Crompton (2006)

Ketambe had higher densities of medium-sized lianas (2-4 cm DBH) which is likely a result of the more fertile Sumatran soils and lack of logging. Contrary to expectations based on past logging history, both Suaq Balimbing and Sabangau had a similar density of large lianas (>4 cm). Suaq Balimbing had a more open canopy, which may have provided a good environment for liana establishment, since most liana species need light to germinate and establish (Putz and Appanah, 1987). Crown overlap was much higher in Sabangau than the other two sites, reflecting the homogeneous size of the trees and high stem density in Sabangau, which is likely to have impeded liana establishment.

In Ketambe orangutans used lianas much more frequently than in Sabangau (18.1% vs 3.8% respectively). Orangutans in Suaq Balimbing also used lianas at a reasonably high frequency (12.8%), although they used a mixture of tree and liana supports much more than observed elsewhere (**??**). Whilst in all three sites orangutans tended to avoid using small lianas (<2 cm diameter), it was only in the two Sumatran sites that orangutans used larger lianas much more than their abundance in the environment. Lianas often link tree crowns together bridging gaps and providing arboreal pathways for animals (Emmons and Gentry, 1983; Grand, 1984). However, in forest that has low liana density, orangutans may be more likely to cross gaps by tree-swaying using vertical trunks (Cant, 1992). This would appear to be the strategy employed by orangutans in Sabangau, where it is probably facilitated by the high total stem density, particularly with regard to smaller and more compliant trees, rather than the lack of lianas. The frequency of tree sway by Sabangau orangutans is higher than observed elsewhere (Table 4.8). Tree-sway is known to be a very efficient travel mode for

orangutans (Thorpe et al., 2007aa), so this strategy may help reduce energy expenditure during travel in this population, which is known to be energetically stressed as a result of the low productivity of the Sabangau forest causing orangutans there to experience long periods of negative energy balance (Harrison et al., 2010). Such a strategy may even help mitigate some of the impacts of habitat disturbance on orangutan populations in this and other areas.

There was a slight preference for tree trunks >20 cm in all three sites, although they were only used more frequently than their abundance would predict in the two peat-swamp forests. It must be noted that the majority of trees >20 cm diameter used during locomotion were less than 40cm diameter (79% Suaq Balimbing and 95% Sabangau). This is important because orangutans must use extended-elbow climbing techniques to climb trunks of large diameter. Extended-elbow climbing has a higher duty factor (the fraction of the cycle in which a particular limb is in contact with the support) and is therefore likely to be more demanding than the flexed-elbow techniques they use to climb smaller diameter supports (Isler and Thorpe, 2003). In both Suaq Balimbing and Sabangau there were only a handful of obervations of vertical climbing using extended-elbow "bear climb" (Table 4.8), the majority of which were associated with entering large feeding trees, or travel within feeding trees. This suggests that orangutans avoided this behaviour where possible, but that where it was essential any increased energetic cost was outweighed by the reward of immediately accessing a valuable food resource. Lianas have been highlighted as an important support for orangutans in Ketambe, enabling them to access large feeding trees without having to employ the more demanding bear climb

required to ascend large tree trunks (Isler and Thorpe, 2003; Thorpe and Crompton, 2005). Despite this, bear climb was observed at slightly higher levels in Ketambe (Table 4.8; Thorpe and Crompton, 2006) than in the two peat-swamp forests, indicating that the smaller girthed trees in these peat-swamps can be climbed using flexed-elbow climb. Climbing was slightly lower in Sabangau than in Suaq Balimbing and Ketambe (Table 4.8), this is likely due to past disturbance resulting in a more stunted canopy thus reducing the incidence of climbing behavior. In the two peat-swamp sites orangutans showed a slight tendency towards using tree trunks for travel (<20 cm diameter), whereas this relationship was slightly negative in Ketambe. This is most likely due to the taller canopy and larger tree size in Ketambe, causing orangutans to travel at higher levels, and the higher density of lianas that can be used as alternative supports.

The use of tree trunks as a support was higher in both of the peat-swamp forest sites than was observed in dry-forest, although it was highest in Sabangau. However, trunks of 4-10 cm in diameter accounted for almost half of all locomotion involving single trunks in both peat-swamp forest sites (46% in Suaq Balimbing; 48% in Sabangau). Tree trunks of this size are flexible and therefore easily oscillated about the trunk, and around 70% of all locomotion on trunks of this size involved tree swaying in both of the peat-swamp forest sites. It would seem that the tendency for orangutans in peat-swamp forest to use vertical trunks reflects both the higher density of smaller sized trunks compared with dry-forest, as well as differences between the sites with regard to the most continuous stratum for travel.

When support availability was compared between the three sites, the two

peat-swamp forests were more similar to each other than to the dry-forest. Ketambe had a more varied range of supports, which supports the hypothesis that orangutans in Ketambe are more able to use particular locomotor/support combinations as a consequence of their more heterogeneous arboreal environment. Interestingly, orangutans in Suaq Balimbing had a much higher frequency of locomotion on multiple supports of the smallest size (<4 cm diameter) than was observed in the other sites. This does not reflect a higher availability of supports of this type, which was the same as for Sabangau. Rather, it reflects the fact that orangutans used different strata in the two peat-swamp sites. Orangutans in Suaq Balimbing crossed trees via small peripheral branches in the crown whereas in the Sabangau they crossed at lower levels using closely spaced trunks, and in Ketambe they benefitted from increased access to larger branches in the crowns of trees. Orangutans in Ketambe had a stronger relationship with single large supports, which is not suprising, as we would expect orangutans to use compressive locomotion on larger, stiffer supports wherever possible because this is likely to reduce the energetic cost and risks of arboreal locomotion (Rosenberger and Strier, 1989; Strier, 1991; Warren and Crompton, 1998). Indeed, orangutans in Ketambe do exhibit higher frequencies of quadrupedal walk than were observed in peat-swamp (Table 4.8). It is therefore likely that the increased frequency of larger horizontal supports in Ketambe facilitates both energetically advantageous locomotor behavior and increased safety. In contrast, orangutans inhabiting peat-swamp forest tended to employ orthograde behaviour (i.e. clambering) and tree-sway on single tree trunks to reduce energy expenditure on travel and increase safety. It is also worth noting here that orangutans travelled lower heights in peat-swamp forest which reduced risk from falls.

Orangutans at all three sites exhibited similar frequencies of locomotion on single supports (4-10 cm), although locomotion on multiple supports of this size class was more frequent in Sabangau than at the other sites, reflecting the frequency of clambering across multiple trunks (chapter 3). Orangutans in all three sites used branches and boughs more than their abundance in all but the smallest size categories, where they similarly avoided the smallest branches (<2 cm). This does not mean that orangutans do not use the smallest supports, however, but rather that they do not use them in proportion to their abundance. Only in Ketambe did orangutans avoid the smallest boughs, whereas in Suaq Balimbing they were a preferred support and in Sabangau they were used in accordance to availability (i.e., neutral selection). These results suggest that orangutans in all forests do select for preferred support/locomotion combinations, but, in more homogeneous forests with a more limited number of support size variation (e.g. Sabangau), orangutans are restricted to a more limited range of preferred locomotion/support combinations (hypotheses 1 and 2). Indeed, that orangutans in Sabangau exhibit higher frequencies of a small number of locomotor behaviors compared to orangutans in both Suaq Balimbing and Ketambe (Table 4.8) indicates that orangutan locomotion is more limited in homogenous forest structure.

Our hypothesis that there would be little variation in the trees used among age-sex classes was upheld in Suaq Balimbing but not Sabangau (hypothesis 3). The lack of difference in the structural features of travel trees in Suaq Balimbing between the various age-sex categories is likely to be a consequence of the use of arboreal pathways, which individuals of all age-sex categories were thought to follow in Ketambe (Thorpe and

Crompton, 2005). This common use of arboreal pathways was also observed in Suaq Balimbing, where individuals travelling together would use the same route when travelling to distant feeding trees (Manduell, personal observations). Focal individuals were also observed to use the same sequence of trees that had been marked from a previous follow of a different focal orangutan (Manduell, personal observations). However, in Borneo the presence of arboreal pathways was less obvious given that orangutans are more solitary. This was observed in both Sabangau (chapter 2) and the geographically close orangutan study site of Tuanan, which is also peat-swamp forest (Phillips, 2011). In Sabangau the same individual was observed to use the same sequence of trees on different occasions (chapter 2), but it is thought that the homogeneous nature of the forest may mean that selecting certain trees is less important, as their greater homogeneity reduced the risk of increased energy expenditure through increased path lengths resulting from deviations from straight-line travel (Temerin and Cant, 1983). Nevertheless, sexually active females in Sabangau used larger trees for travel than the other age-sex categories. Previous studies have indicated that sexually active females tended towards safer forms of locomotion (Thorpe and Crompton, 2005; chapter 2) and this result supports that suggestion.

Our prediction that there would be differences in the trees used for travel between the two peat-swamp forest sites as a result of differences in forest structure was upheld (hypothesis 4). Overall, orangutans selected larger trees for travel in Suaq Balimbing than in Sabangau and, whilst we expected the average distance between consecutive travel trees to be smaller in Sabangau given the much higher stem density, the lack of difference in gap

sizes between the two peat-swamp forests was surprising. We also expected that orangutans in Sabangau would encounter larger gaps between trees given the past logging disturbance, but rather the results from the random sample highlighted the openness of the forest canopy in Suaq Balimbing compared to Sabangau. The similarity in mean gap size between crowns of adjacent travel trees in Suaq Balimbing and Sabangau may indicate a maximum threshold for gap crossing by orangutans, although further testing would be required in order to verify this wasn't simply the maximum distance observed in this study.

It is possible that locomotor strategies could alter in response to food availability. Orangutans in all three sites included in this study employ a "search and find" foraging strategy, as fruit availability is relatively regular with less pronounced peaks and troughs, but is of a typically relatively poor quality (Morrogh-Bernard et al., 2009). However, in Borneo orangutans are more dependent on lower quality fallback foods, and particularly bark, during periods of food scarcity than in Sumatra (Wich et al., 2006; Morrogh-Bernard et al., 2009; Harrison and Marshall, 2011). For much of the duration of the data collection in Sabangau, the orangutans were heavily reliant on fallback foods, such as leaves and bark. Thus, it is possible that, during periods of higher fruit consumption, Sabangau orangutans use arboreal pathways for travelling between preferred known food sources in order to minimize path length, but that during periods of fruit scarcity travel paths are more random, potentially leading to a higher success rate in finding valuable yet previously unknown food sources (Morrogh-Bernard et al., 2009).

As predicted, the attributes of trees used for travel in Sabangau did not differ greatly from the random tree sample, as a result of the more homogeneous forest structure in this site (hypothesis 5). Furthermore, our prediction that orangutans in Suaq Balimbing would select for larger trees for travel than were typically available in the forest was also upheld (hypothesis 6). In order to minimize deviations from direct line travel and increase safety, orangutans in Suaq Balimbing may select for larger trees and travel through the canopy on branches and boughs. Because of the higher availability of fruit at this site (Marshall et al., 2009), orangutans may receive less additional benefit in terms of finding unknown food sources from non-straight line travel than that hypothesised above for Sabangau orangutans. The high use of multiple small supports observed in Suaq Balimbing further reflects the supports used when crossing between trees via the smallest terminal branches of tree crowns. Using larger trees, with associated larger tree crowns, may reduce the gap size between adjacent tree crowns, thereby reducing the need for vertical displacement during travel. In contrast, Sabangau orangutans travelled lower in the canopy, using trunks to cross from tree to tree either by clambering across closely spaced trees or using their weight to sway across to the next tree (chapter 3).

Aside from instances of very fast travel during mating or fighting pursuits, or play, the locomotor behavior of orangutans is in all likelihood a balance between increasing safety and decreasing energy expenditure. Orangutans that are more energetically stressed (e.g. Sabangau) are likely to have to find a compromise between energetic cost and locomotor/support combinations that provide increased safety, whereas in forests where fruit productivity is higher (e.g. Sumatra) orangutans may be able to place greater emphasis on

safety. Orangutans in Sabangau certainly use very high levels of tree sway, whereas orangutans in Ketambe use more compressive locomotion on large supports, which is both energetically efficient and safe. However, orangutans in Suaq Balimbing use larger trees than typically available, presumably to increase safety, but also use multiple small supports at much higher levels than observed elsewhere. Whilst small supports are likely to be less efficient energetically than large supports, they may provide more direct routes to known food sources and therefore increase efficiency by reducing path length. Orangutans have adapted to the unstable environments in which they live by becoming low-energy specialists, decreasing their energy needs when food is scarce (Pontzer et al., 2010), however, it appears that orangutans also adapt their locomotor strategies to reduce the energetic cost of travel more frequently in forests where food availability is lower. These approaches are complementary and could increase the ability of orangutans to survive in habitats where food-energy availability is limited, due to either naturally low nutrient availability and/or anthropogenic disturbance.

The response of primates to habitat structure variables and their ability to either adapt to, or maintain consistency through the selection of preferred supports is both interesting and important, especially in light of increasing impacts of human disturbance on forest structure. Not all primate species respond in the same way to alterations in habitat structure. The positional behaviour of red colobus monkeys (*Colobus badius*) showed greater differences in the context of forest type than in seasonal or annual comparisons (Gebo and Chapman, 1995). Across three species of lemur, positional behaviour and support use were also found to differ between two

forest habitats, but although all three lemur species studied altered in a similar direction, the degree of change was different between species (Dagosto and Yamashita, 1998). In contrast, the locomotor profiles of moustached tamarin monkeys (*Saguinus mystax*) and five cercopithecid species remained consistent in structurally different forests (Garber and Pruetz, 1995; McGraw, 1996). The level of contrast between different habitat types will undoubtedly affect the amount of influence on positional behaviour, as particular habitat features may matter to a greater or lesser extent in different species.

The results of this study indicate that, whilst orangutans in degraded forest (Sabangau) appear to have retained their behavioural repertoire from more optimal habitats (e.g. the two Sumatran sites), they also have adapted to the more homogeneous environment by exploiting the high density of small trees to lower the energetic cost of locomotion, further highlighting the value of logged forests for orangutan conservation efforts.

4.5 Conclusions

The three sites used in this study showed a large degree of difference in terms of tree and liana density. As predicted, Ketambe and Sabangau showed the greatest degree of variation, and Suaq Balimbing was more similar to Sabangau in terms of structural features, particularly with regard to support availability. Contrary to our prediction, orangutans across all three study sites had an essentially similar profile of preferred supports, with the most notable exception being Sumatran orangutans' stronger propensity for using lianas, which was not observed in the Borneo site. Orangutans in Sabangau had a more limited repertoire with high

frequencies of a few behaviors, compared to the two Sumatran sites, whereas the wider range of supports in Ketambe appears to have facilitated a more varied locomotor repertoire. In Sumatra orangutans clearly used arboreal pathways for travel, as indicated by the lack of difference between the age-sex classes and the selection of larger trees than typically available. This was less apparent in Borneo, where sexually-active females selected larger trees, presumably for increased safety, and where, in general, trees used were similar to those present in the site, reflecting the more structurally homogeneous nature of disturbed peat-swamp forest.

The results of this study demonstrate that forest structure and support availability have important effects on orangutan locomotion. This influence is likely to become increasingly important as forest structure continues to be altered through human disturbance in many areas. The travel pattern observed in Sabangau probably helps reduce energy expenditure through travel, which might be expected to help orangutans cope with the changes in habitat structure and reduced availability of food resources, and therefore energy intake, that accompanies habitat disturbance.

CHAPTER 5

Size Matters: The Comparative Limb Morphology of Wild Orangutans (*Pongo abelii* and *Pongo pygmaeus wurmbii*)

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KLM collected the measurements from Ketambe, Suaq Balimbing and Sabangau, developed the methods, analysed the data and wrote the manuscript, ACP collected the measurements from Tuanan and developed the methods, FS collected the measurements from Nyaro Menteng, SKST assisted in the development of the methods and the writing of the manuscript

ABSTRACT

The relationship between the functional anatomy of an animal, and its behavior and habitat use are paramount in understanding how the external environment influences morphology. In this study we investigated both inter- and intra-specific differences in limb lengths of wild orangutans (*Pongo abelii* and *Pongo pygmaeus wurmbii*). Despite differences in cranial morphology that result from a disparity in the quality of diet between Borneo and Sumatra, no differences in limb lengths were observed between the two species. This indicates that an optimal limb length for both fore- and hindlimbs is selected for as it is likely to confer benefits for an arboreal lifestyle, and particularly gap crossing behavior, which may outweigh the additional energetic cost associated with maintaining large body size. Male orangutans are larger than females, although little difference was observed between flanged and unflanged males suggesting that the development of secondary sexual characteristics in orangutans is associated with weight gain rather than skeletal growth *per se*. No differences were observed between age-sex classes in measurements adjusted for body mass indicating that male and female orangutans are isometrically similar.

5.1 Introduction

It is estimated that Bornean and Sumatran orangutans diverged between 2.7 – 5 mya (Steiper, 2006) and they are currently classified as two separate species, *Pongo abelii* in Sumatra and *Pongo pygmaeus* in Borneo. The Bornean orangutan is further classified into three geographically separated sub-species; *P. pygmaeus pygmaeus* in Northwest Kalimantan and Sarawak, *P. p. morio* in East Kalimantan and Sabah and *P. p. wurmbii* in West, South and Central Kalimantan (Xu and Arnason, 1996;Zhi et al., 1996; Groves, 2001; Singleton et al., 2004; Goossens et al., 2009).

Inter-specific differences have been documented for brain size (Taylor, 2006; Taylor and van Schaik, 2007), craniofacial morphology (Groves and Shea, 1992; Taylor, 2006) and dental morphology (Uchida, 1998). Brain tissue is metabolically expensive as the growth and maintenance of large brains requires either a large energy input (Martin, 1996; Fish and Lockwood, 2003) and/or a decrease in other energetically expensive tissues (Aiello and Wheeler, 1995; Isler and Van Schaik, 2006) thus the differences in cranial morphology between orangutan species and sub-species have been related to differences in forest productivity. Bornean orangutans frequently experience nutritional stress whereas Sumatran orangutans have not been observed to catabolise their fat reserves (Harrison et al., 2010; Knott, 1998; 1999; Wich et al., 2006). Bornean orangutans have smaller brains and stronger mandibles than Sumatran orangutans that fits with a gradient of reduced fruit availability, increased frequency of periods of fruit scarcity and therefore heavier reliance on bark as a fallback food from west to east (Taylor, 2006; Taylor and van Schaik, 2007; van Schaik et al., 2009). The Bornean sub-species *P. p morio*, which experiences the most prolonged lean

fruiting periods and therefore relies more heavily on hard foods such as bark, has the most robust mandible and the smallest brain (Taylor and van Schaik, 2007). In contrast, Sumatran orangutans exist on a fruit dominated diet as a result of the higher productivity and higher density of fig trees, and have the most gracile mandible and largest brain, whereas *P. p. wurmbii* which exhibits intermediate levels of frugivory falls between *P. abelii* and *P. p. morio* in terms of both brain size and mandibular robusticity (Taylor, 2006, 2009; Taylor and van Schaik, 2007).

Whilst the two species are reportedly of broadly similar size (Markham and Groves, 1990) there are no comparative measurements of their postcranial anatomy and even relatively recent studies investigating the postcranial morphology of primates have not differentiated between orangutan species (e.g. Shaw and Ryan, 2012). Despite the fact that differences in forest productivity have resulted in a relationship between energy intake, feeding behaviour, mandibular robusticity and brain size (Taylor, 2006, 2009; Taylor and van Schaik, 2007), we still know little about whether orangutan species differ postcranially (Thorpe and Crompton, 2009). Based on differences in brain size, we might expect a similar west to east gradient in terms of size, with Sumatran orangutans, as a result of their higher quality diet, being larger than their Bornean counterparts. In addition, the lower productivity of Bornean forests have been hypothesised to influence the body size of a number of mammal species such as the Malayan sun bear (*Helarctos malayanus*), the greater chevrotain (*Tragulus napu*), sambar (*Cervus unicolor*) as well as the carnivores (Meijaard, 2004; Meijaard and Groves, 2004a, b; Meiri et al., 2008). However, since it is generally agreed that the living apes form a biological lineage defined by characters of the locomotor system

(trunk and upper limbs) rather than the cranial and dental features that define many other mammalian groups, understanding inter-specific variation in orangutan postcranial morphology is fundamental to elucidating the ecological and locomotor diversity of the genus.

Variation in the proportions of the proximal (i.e. humerus and femur) and distal (i.e. radius/ulna and tibia/fibula) segments are generally correlated with significant differences in positional behaviour (Fleagle, 1999). However, comparative studies of the positional behaviour and postcranial morphology of closely related primates have shown that even subtle differences in positional behaviour may be capable of altering skeletal morphology (Wright, 2007; Fleagle, 1999;Glassman, 1983; Rodman, 1979a; Ward and Sussman, 1979). Thorpe and Crompton (2009) note that if differences in positional behaviour of closely related species are sufficiently large, or occur with sufficient frequency, it may be expected to be expressed in differences in the anatomy of the locomotor system. Previous studies investigating the positional behavior of wild orangutans found the same overall locomotor repertoire for both species, yet they did exhibit different frequencies of locomotor behaviors (Thorpe and Crompton, 2006; chapter 2, chapter 4). Bornean orangutans employed more orthograde suspensory locomotion and tree sway than was observed in Sumatra, and generally exhibited higher frequencies of fewer behaviors when compared to their Sumatran counterparts (chapter 4). In chapter 4 we suggested that many of these differences in observed locomotor behaviour were caused by gross differences in forest structure and support availability since overall orangutans exhibited similar profiles of preferred supports during locomotion. Therefore, we might expect that any differences in orangutan

postcranial morphology will be driven by differences in the quality of diet between the two islands rather than locomotor behaviour.

Limb indices reflect proportions of long bone lengths within and between segments, as opposed to absolute lengths and are thus useful for describing body proportions of a species as they are considered to be correlated with locomotor differences in many primates (Fleagle and Meldrum, 1988; Aiello and Dean, 1990; Fleagle, 1999). For example, the intermembral index which is a measure of the relative length of the forelimb and hindlimb is generally low in leaping primates, intermediate in quadrupedal primates and high in suspensory primates (Fleagle and Meldrum, 1988). Among large-bodied hominoids, orangutans have the highest intermembral index reflecting their long forelimbs and short hindlimbs (Jungers and Hartman, 1988). The elongated forearm is thought to be a response to selection for their highly specialised locomotor behaviour (Schultz, 1933) and the benefits of an elongated forelimb for suspensory behavior have been widely documented (e.g. Jungers and Stern, 1984; Preuschoft and Demes, 1984; Oishi et al., 2008). Certainly elongated forelimbs provide greater reach between arboreal supports (Tuttle, 1975; Preuschoft and Demes, 1985) as well as increased reach during foraging (Grand, 1972). Orangutan locomotor behaviour is predominantly orthograde suspension whereby the body is orthograde with the head superior, and various combinations of all four appendages grasping supports in different ways, with suspension by the forelimbs from above (Cant, 1987b; Thorpe and Crompton, 2005, 2006; chapter 2). The combination of long forelimbs with short hindlimbs confers further benefits in an arboreal environment, particularly for suspensory locomotion involving multiple weight-bearing supports, as it enables both long-range

(forelimb) and short-range (hindlimb) grasping, thus orangutans are able to increase the range of potential weight bearing supports (Rose, 1988).

Limb proportions are not only determined by locomotor morphology, but also sexual size dimorphism (Clutton-Brook and Harvey, 1978). Orangutans show extreme sexual dimorphism with flanged males weighing between (80-91kg), more than twice that of adult females (33-45kg) (Figures based on Bornean orangutans only - Markham and Groves, 1990). In addition to extreme sexual dimorphism orangutans also have pronounced bimaturism with males exhibiting two distinct morphs, flanged and unflanged, which are thought to represent two well defined mating strategies, "call and wait" by flanged males, and "sneak and rape" by unflanged males (Delgado and van Schaik, 2000; Harrison and Chivers, 2007). Sexual dimorphism in brain size between males and females of the Bornean sub-species *P. p morio* has been documented with males having larger relative brain size compared to females. This has been attributed to the smaller home ranges of adult females resulting in greater nutritional risk as a result of pregnancy and lactation (Taylor, 2009). Orangutans were found to have marked sexual dimorphism in body mass and linear measurements, male and female orangutans differ in their hindlimb proportions (Morbeck and Zihlman, 1988; Zihlman and McFarland, 2000), although this was for an extremely small sample size. However, long bone indices presented in Aiello and Dean (1990) show similar values for male and female orangutans. Based on this we might expect to see differences in limb lengths between age-sex classes in orangutans, which mirror body mass. However, when measurements are scaled to body size we would expect them to be isometrically similar with males essentially being larger versions of females.

The majority of data on postcranial morphology and their association with locomotor behaviour are generally obtained from disarticulated bones from museum specimens (e.g. Rodman, 1979a; Fleagle and Meldrum, 1988; Gebo and Sargis, 1994; Glassman, 1983, Wright, 2007), although some studies have anesthetized living animals in order to take measurements (e.g. Garber and Leigh, 2001; Anapol et al., 2005). Obtaining segment length measurements from wild animals is important as the impoverishment of captive environments has the potential to modify the musculo-skeletal development of an animal during the course of its lifetime (Sarmiento, 1986). However, recent advances in the measurement of morphological traits under wild conditions have yielded accurate dimensions and has been used to measure the shoulder heights of African elephants, *Loxodonta Africana* and assess sexual dimorphism in wild western gorillas, *Gorilla gorilla* (Shrader et al., 2006; Breuer et al., 2007; Caillaud et al., 2008). The parallel laser technique, where lasers are situated a known distance apart and when projected onto an object provide a scale bar from which measurements can be made, has also been used for a variety of biological applications, such as measuring the horn growth of free-ranging Alpine ibex (*Capra ibex*), dorsal fin size in both free-ranging killer whales (*Orcinus orca*) and bottlenose dolphins (*Tursiops sp.*) and the tail lengths of red colobus monkeys, *Procolobus rufomitratus* (Bergeron, 2007; Durban and Parsons, 2006; Rothman et al., 2008; Rowe and Dawson, 2009).

In this study, we assessed differences in limb proportions between age-sex classes from wild-caught rescued orangutans. Given the large degree of sexual dimorphism and bimaturism in orangutans we hypothesise that 1) there will be a difference in limb proportions between the age-sex classes

that mirror mass, but 2) when scaled for body size there will be little difference between age-sex classes. We also examine evidence of species differences in limb proportions between the two orangutan species, *Pongo abelii* in Sumatra, and the sub-species *P. p. wurmbii* in Borneo using the parallel laser technique. Specifically we hypothesise that 3) any difference in postcranial morphology will be due to the lower quality diet in Borneo, rather than reflecting differences in locomotor behaviour.

5.2 Methods

Measurements of the physical traits were obtained for *Pongo abelii* in Sumatra and the sub-species *Pongo pygmaeus wurmbii* in Central Kalimantan, Borneo. Measurements were obtained in four orangutan study sites, two on Sumatra - Ketambe (3° 41′ N, 97° 39′ E) and Suaq Balimbing (3° 42′ N, 97° 26′ E); and two on Borneo - Sabangau (2° 03′ S, 113° 54′ E) and Tuanan (2° 09′ S, 114° 26′ E). Information on the study sites are presented in Table 5.1. Further measurements were obtained for the sub-species *P. p. wurmbii* from the Borneo Orangutan Society (BOS) Nyaro Menteng rehabilitation centre in Central Kalimantan, for wild-caught orangutans, who were later translocated. Four age-sex classes were used in this study: flanged males were fully mature males that had developed secondary sexual characteristics such as cheekpads and throat pouches; sexually active females were those with dependent infants or old enough to have produced offspring whether in parturition or not; non-sexually active females includes adolescent females which have not yet borne offspring and unflanged males includes both unflanged adult males and independent, non-sexually active males (adapted from Morrogh-Bernard et al., 2009).

Table 5.1 – Overview of Study Sites

	Sabangau	Tuanan	Suaq Balimbing	Ketambe
Location	Central Kalimantan, Borneo	Central Kalimantan, Borneo	Gunung Leuser, Aceh Sumatra	Gunung Leuser, Aceh, Sumatra
Species	*Pongo pygmaeus wurmbii*	*Pongo pygmaeus wurmbii*	*Pongo abelii*	*Pongo abelii*
Forest Type	Peat-Swamp	Peat-Swamp	Peat-Swamp	Dry Lowland
Canopy Height[a,b]	15-25 m	15-25 m	15-25 m	35-40 m
Disturbance	Logged	Logged	Unlogged	Unlogged
Productivity	Low	Low	High	High
Rainfall[c]	2,790 mm	3,010 mm	3,400 mm	3,288 mm
Mean Elevation[c,d]	10 masl	2 masl	10 masl	320 masl upwards
Orangutan Standardised Density[d]	2.35 ind/km^2	3.84 ind/km^2	7.44 ind/km^2	3.24 ind/km^2

[a] Page et al. (1999)
[b] Whitmore (1984)
[c] Wich et al (2009)
[d] Husson et al (2009)

Measurements were taken using a remote measuring technique whereby parallel lasers were attached at equal fixed distances apart (4 cm) to an L-shaped aluminium frame (following Rothman et al., 2008; Bergeron, 2007) on which a digital camera (Nikon D90SLR) and clinometer (Silva Clinomaster) were mounted in a fixed position. We also added a third laser to confirm the distance apart on both axes to account for any potential disparity between pixel width and length (Figure 5.1). Validation of the laser technique was done with the assistance of an experienced tree climber who manually measured the distance (to the nearest mm, n = 30) between markers on tree branches in the forest canopy (Figure 5.2a). These measurements were then compared with those obtained from the digital photographs with the parallel laser projections.

During the course of nest-to-nest follows of wild orangutans, the parallel lasers were projected onto target limbs and a photograph taken (Figure 5.2b).

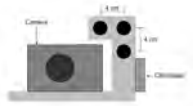

Figure 5.1 – Diagram of the apparatus used to perform the parallel laser technique, which includes an aluminium frame with three lasers set at a know distance (4 cm). A digital camera and clinometer are attached to the frame in a fixed position. The laser beams were regullarly callibrated to ensure they were 4 cm apart. The technique was validated using laser projections on tree branches where precise measurements were taken manually.

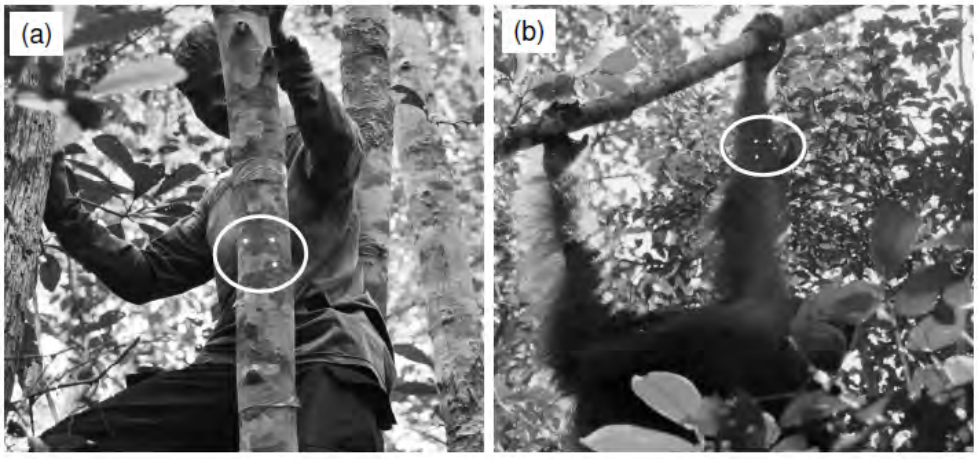

Figure 5.2 – Photographs of a) the validation technique using laser projections on tree branches with known measurements between markers; b) the lasers projected onto the limb of an orangutan.

In order for this method to produce accurate measurements of orangutan limbs, it was necessary for the target limb to be perpendicular to the ground (i.e. surfaces are vertical). Whilst the lasers used are classified as IIIA and there are no known risks of injury associated with exposure to human eyes, every effort was made to ensure that the lasers were not shone near the facial area of focal animals in order to avoid any potential damage to their eyes. The clinometer is a necessary component of the apparatus as when the lasers are aimed at an angle, the length of the higher beam is longer than the length of the lower beam thereby altering the actual distance between the two laser

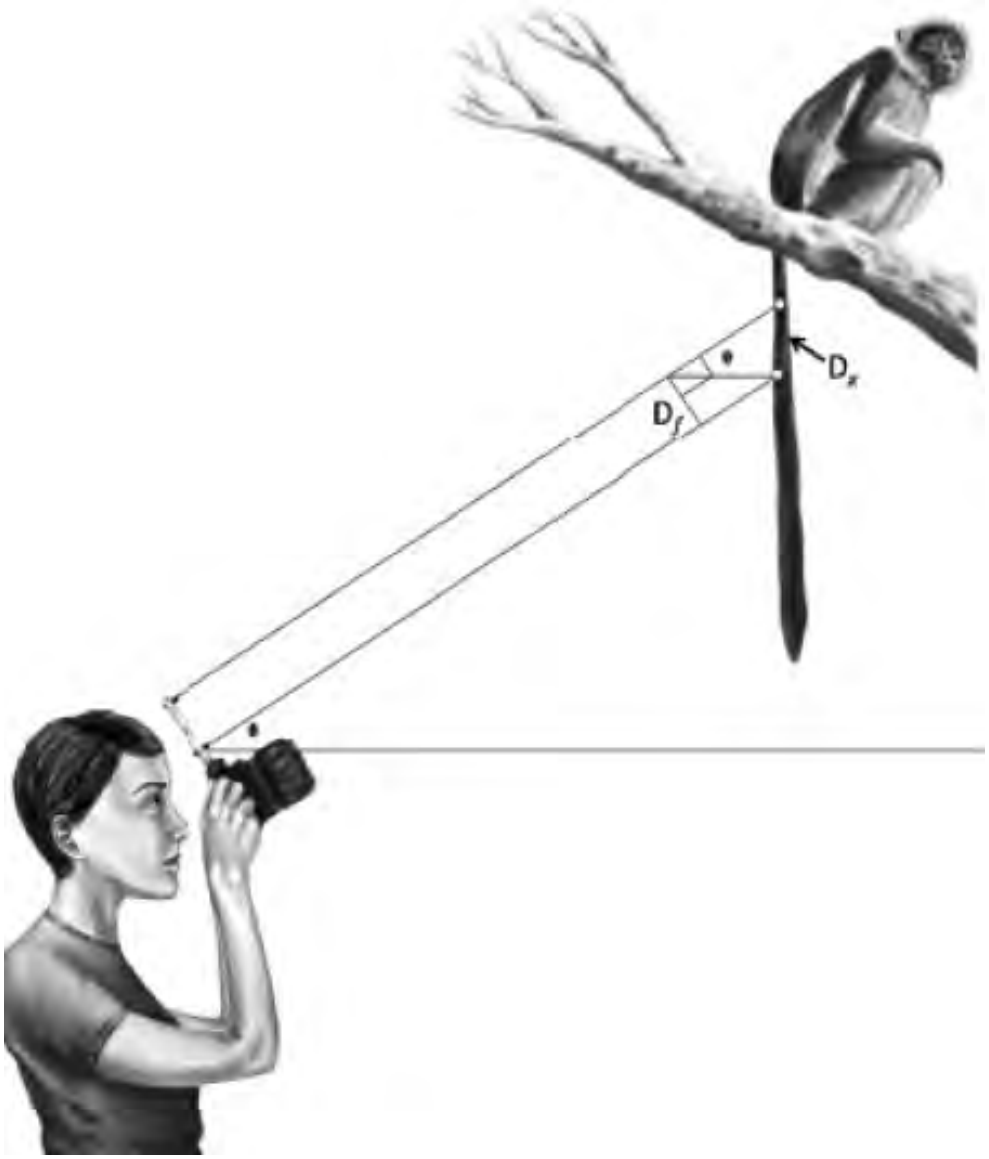

Figure 5.3 – The use of lasers to measure physical traits of arboreal primates. The laser beams provide a visible scale bar from which measurements can be obtained (taken from Rothman et al., 2008, pg 1194)

projections. By knowing the camera angle this disparity in distance between the laser beams can be factored into the calculations (Figure 5.3).

Limb Measurements

When taking measurements using the remotely projected parallel lasers, we used physical markers that were visible in photographs to ensure consistent measurements were obtained. The forearm was measured from the styloid process to the olecranon; the arm was measured from the olecranon to the head of the humerus, the crus was measured from the ankle (medial malleolus) to the knee cap (patella) and the thigh was measured from the knee cap (patella) to the back of the hip joint (Figure 5.4). The total forelimb length was the sum of the forearm and arm, and the total hindlimb length was the sum of the thigh and crus. The measurements obtained manually from live orangutans in Nyaro Menteng were: forearm, from the olecranon of the elbow to the prominent wrist bone, along the back of the arm; arm, from the head of the humerus to the olecranon (point of the elbow), along the outside of the arm; crus, from the patella (knee cap) to the prominent ankle bone, along the outside of the leg; and thigh, from the back of the hip joint to the patella (knee cap) along the outside of the leg.

The lengths of limb bones for an individual provide a basis for calculating indices that reflect proportions within and between limb segments of that individual (Zihlman et al., 2008). Several indices were calculated from the measured variables: "intermembral" index, 100 x (arm + forearm)/(thigh + crus); "humerofemoral" index, 100 x arm/thigh; "brachial" index, 100 x forearm/arm; "crural" index, 100 x crus/thigh. Since the majority of published data on the postcranial anatomy tends to be derived from measurements of bones rather than living specimens, the measurements obtained for this study are likely to provide slightly different, yet proportionately equivalent values compared to those obtained from bone

Figure 4. Measurements from digital photographs using the parallel laser technique.

Figure 5.4 – Measurements from digital photographs using the parallel laser technique

measurements (Anapol et al., 2005).

Photograph Analysis

Using the scale bar produced by the parallel laser beams (4cm apart) on each photograph, together with the angle of the lasers, the target limb was measured using the formula:

$$T_a = \frac{(T_r \times L_a)}{L_r}$$

(following Rothman et al., 2008)

where, T is the measurement of the target limb and L is the distance between the two lasers, the subscript r is the remote measurement and the subscript a is the actual hand measurement. In order to account for the difference in path length between laser beams when projected at an angle, a clinometer will be used to measure the angle (θ) between the lower laser when projected onto the target object and the horizontal. This difference in distance can then be corrected using the formula:

$$D_x = D_f \text{ x } \tan \theta \cos (90 - \theta)$$

where D is the distance between the lasers, is the angle θ of the projected lower laser beam on the subject with the horizontal, f is the fixed distance between the lasers (4cm) and x is the unknown distance of the lasers when projected onto the target object. D_x is then substituted back into the original equation as L_a.

The weight of each individual were also collected for the BOS Nyaro Menteng sample allowing us to correct for differences in body size, while preserving size-related shape information, between each age-sex class. Each limb segment was normalised by dividing its length by the cube root of body weight (Sneath and Sokal, 1973; Emerson, 1985; Jungers, 1985a; Garber and Leigh, 2001; Anapol et al., 2005). However, measurements obtained using the parallel laser technique could not be allometrically corrected as we could not weigh the individuals, therefore the relative, or scale-free variations in limb segments were compared.

Statistical Analysis

Pearson's rank correlation was used to test whether the percent error in measurement was correlated with the distance between markers on branches. Student's t-test or one-way ANOVA (with Tukey post hoc) was used to compare data, where data did not violate assumptions of normality and heterogeneity of variance, otherwise variables were compared using Kruskal-Wallis non-parametric test and the Mann-Whitney U-test test post hoc. Given the need for multiple comparisons in the Mann-Whitney U-test, the significance level was lowered according to Bonferroni probabilities (dividing the Type I error rate, e.g. 0.05, by the number of comparisons; Field, 2005). Photographs were downloaded into GIMP version 2.6 and the 'measure tool' was used to measure both branch length and limb proportions. All computations and statistical analysis were undertaken using SPSS version 19.0.

5.3 Results

Nyaro Menteng

We obtained measurements of 80 individuals of the Bornean sub-species *P. p. wurmbii* from BOS Nyaro Menteng, means and standard deviations for all measurements and calculated long bone indices are presented in Table 5.2. In the non-size adjusted measurements flanged males had significantly longer limb segments than sexually active females and non-sexually active females. However, with the exception of the length of the arm, the length of limbs in flanged males were similar to unflanged males (Table 5.3). No significant differences in limb length were observed between sexually active females and non-sexually active females, but both were significantly smaller

Table 5.2 – Means (+ standard deviation) with calculated indices for Nyaro Menteng and laser measurements

	P. p. wurmbii			*P. p. wurmbii*			*P. abelii*		
	Nyaro Menteng			Sabangau & Tuanan			Ketambe & Suaq		
	n	Mean	Std Dev	n	Mean	Std Dev	n	Mean	Std Dev
Forearm	80	34.39	(3.58)	15	35.46	(4.49)	15	37.22	(3.94)
Arm	80	32.84	(3.52)	15	31.61	(5.16)	15	34.59	(4.39)
Thigh	80	25.10	(2.61)	15	25.83	(3.95)	11	26.85	(3.74)
Crus	80	23.96	(2.54)	15	24.23	(3.95)	12	26.40	(3.51)
Forelimb	80	67.23	(7.04)	15	66.60	(9.32)	15	71.80	(8.23)
Hindlimb	80	49.06	(5.10)	15	50.06	(7.81)	11	52.93	(7.16)
“Intermembral” index	80	137.45	(10.50)	15	133.69	(11.70)	12	135.84	(13.53)
“Humerofemoral” index	80	131.24	(10.39)	15	129.10	(14.55)	12	133.27	(13.30)
“Brachial” index	80	104.79	(2.76)	15	114.90	(10.86)	15	107.98	(4.89)
“Crural” index	80	95.48	(2.84)	15	93.80	(4.65)	11	97.30	(3.97)

than unflanged males for all limb segments (Table 5.3). No significant differences between the four age-sex classes were observed for any of the calculated long bone indices (Table 5.4).

Flanged males had a mean weight of 67.4 kg (range: 59-85 kg) and were significantly heavier than the other age-sex classes (Table 5.5) weighing approximately 1.5 times more than unflanged males (46.3 kg; range: 30-75 kg), and more than twice as much as sexually active (32.7 kg; range: 24-46kg) and non-sexually active females (26.9 kg; range 20-39 kg). There was no significant difference in the weight of sexually active females and non-sexually active females (Table 5.5). No significant differences in the limb proportions between the age-sex classes were found for size-adjusted measurements of forearm, arm, thigh, crus, forelimb or hindlimb (Table 5.5).

Validation

The mean distance between markers placed on tree branches in the forest canopy using manual measurements was 28.65 ± 3.05 cm (range: 6.6 – 71.8 cm) , and using the parallel laser projection measurements from digital photographs was 28.56 ±3.04 cm (range: 6.44 – 71.5 cm). The mean error was 0.22 ±0.18 cm (range:-0.5 – 0.7 cm). The average error was 0.89% of the mean length, and the largest error in a single measurement was 2.42%. The distance between the markers on tree branches was not correlated with error in measurement (Pearson's r=1.141, P=0.456) and there was no difference between branches measured manually or via digital photographs (t=-1.854, df=29, P=0.074).

Table 5.3 – Comparison of actual limb measurements between age-sex classes measured at Nyaro Menteng

	Kruskal-Wallis		Age-sex Class (Means)				Mann-Whitney U-Test (*post hoc*)					
	(H)		FM	SAF	UFM	NSAF	1 vs	1 vs	1 vs	2 vs	2 vs	3 vs
	1 vs 2 vs 3	P	(1)	(2)	(3)	(4)	2	3	4	3	4	4
			(n=6)	(n=29)	(n=24)	(n=21)						
Forearm	24.175	***	39.50	33.03	36.21	32.71	***	ns	***	**	ns	**
Arm	24.539	***	38.50	31.62	34.42	31.10	***	*	***	*	ns	**
Thigh	21.516	***	28.17	24.21	26.54	23.81	***	ns	***	**	ns	*
Crus	24.043	***	26.83	23.03	25.33	22.86	***	ns	***	**	ns	**
Forelimb	24.994	***	78.00	64.66	70.63	63.81	***	ns	***	**	ns	**
Hindlimb	23.060	***	55.00	47.24	51.86	46.67	***	ns	***	**	ns	**

FM, flanged males; SAF, sexually active female; UFM, unflanged male; NSAF, non-sexually active female
Kruskal-Wallis: *P≤0.05; **P≤0.01; ***P≤0.001; ns, not significant

Mann-Whitney U-test (according to Bonferroni probabilities): *P≤0.0125; **P≤0.0025; ***P≤0.00025

Table 5.4 – One-way analysis of variance and means separation tests for calculated indices from Nyaro Menteng measurements

				Age-Sex Class (Means)				Tukey's Test *post hoc*					
				FM	SAF	UFM	NSAF	1 vs	1 vs	1 vs	2 vs	2 vs	3 vs
	F	DF	P	(1)	(2)	(3)	(4)	2	3	4	3	4	4
"Intermembral" index	0.452	3	0.717	141.89	137.72	136.34	137.09	ns	ns	ns	ns	ns	ns
"Humerofemoral" index	0.749	3	0.526	136.75	131.48	129.86	130.91	ns	ns	ns	ns	ns	ns
"Brachial" index	1.788	3	0.157	102.61	104.53	105.26	105.22	ns	ns	ns	ns	ns	ns
"Crural" index	0.335	3	0.800	95.25	95.18	95.47	95.99	ns	ns	ns	ns	ns	ns

FM, flanged male; SAF, sexually active female; UFM, unflanged male; NSAF, non-sexually active female

Tukey's Test post hoc: *P≤0.05; **P≤0.01; ***P≤0.001; ns, not significant

Table 5.5 – One-Way Analysis of Variance and Means Separation Tests for Size-Adjusted Measurements Taken at Nyaro Menteng

				Tukey's Test *post hoc* [a]					
				FM	FM	FM	SAF	SAF	UFM
Variable	F	df	P	vs SAF	v UFM	v NSAF	V UFM	v NSAF	v NSAF
Weight	33.995	3	0.000	***	***	***	***	ns	***
Forearm	1.441	3	0.239	ns	ns	ns	ns	ns	ns
Arm	1.844	3	0.148	ns	ns	ns	ns	ns	ns
Thigh	1.619	3	0.193	ns	ns	ns	ns	ns	ns
Crus	2.139	3	0.104	ns	ns	ns	ns	ns	ns
Forelimb	1.629	3	0.193	ns	ns	ns	ns	ns	ns
Hindlimb	2.152	3	0.103	ns	ns	ns	ns	ns	ns

FM, flanged male (n = 5); SAF, sexually active female (n = 22); UFM, unflanged male (n = 23); NSAF, non-sexually active female (n = 19)

[a] Tukey's Test *post hoc*: *P≤0.05; **P≤0.01; ***P≤0.001; ns = not significant

Table 5.6 – Means (+ standard deviation) from male laser measurements and calculated indices

	P. abelii			*P. p. wurmbii*					
	n	Mean	S.D.	n	Mean	S.D.	t	df	P
Forearm	5	41.62	(2.78)	7	37.16	(5.60)	1.627	10	0.135
Arm	5	39.62	(2.09)	7	33.41	(6.75)	1.966	10	0.078
Thigh	5	30.50	(2.85)	7	28.14	(4.62)	0.804	8	0.445
Crus	4	29.92	(1.46)	7	26.47	(4.42)	1.484	9	0.172
Forelimb	3	81.24	(4.83)	7	70.57	(12.14)	1.843	10	0.095
Hindlimb	3	60.43	(4.61)	7	54.60	(8.99)	1.039	8	0.329
"Intermembral" index	4	133.53	(14.43)	7	129.33	(11.29)	0.539	9	0.603
"Humerofemoral" index	4	132.78	(12.29)	7	126.05	(15.27)	0.749	9	0.473
"Brachial" index	5	104.99	(2.22)	7	112.62	(11.14)	-1.489	10	0.167
"Crural" index	3	98.37	(3.94)	7	94.08	(3.47)	1.727	8	0.122

Inter-specific Differences

Using the parallel laser technique, measurements from fifteen individuals were obtained for adult orangutans in Sumatra (*P. abelii*), six from Ketambe and nine from Suaq Balimbing; measurements of fifteen adult orangutans were also obtained in Borneo (*P. p. wurmbii*), nine from Sabangau and six from Tuanan (Table 5.2).

Inter-specific comparisons between the pooled laser measurements for *P. abelii* and *P. p. wurmbii* revealed no significant differences for any of the variables measured (Student's t-test, $P<0.05$). Based on the results from the Nyaro Menteng measurements we pooled sexually active females and non-sexually active females together, and flanged males and unflanged males together. No significant differences were found between male *P. abelii* and *P. p. wurmbii* for any of the limb measurements or calculated long bone indices (Table 5.6). No significant differences were found between female *P. abelii* and *P. p. wurmbii* for any of the limb measurements or calculated long bone indices (Table 5.7).

5.4 Discussion

The dataset obtained from Nyaro Menteng represents the largest sample of weights and measurements of wild orangutans to date. The large degree of sexual dimorphism and bimaturism in orangutans led us to predict that there would be differences in size between all four age-sex classes included in this study. However, whilst flanged males are considerably heavier than unflanged males, only the arm (humerus) of flanged males was significantly longer. Unflanged males were previously considered to be of a similar size

Table 5.7 – Means (+ standard deviation) from female laser measurements and calculated indices

	P. abelii			*P. p. wurmbii*					
	n	Mean	S.D.	n	Mean	S.D.	t	df	P
Forearm	10	35.02	(2.15)	8	33.98	(2.82)	0.895	16	0.384
Arm	10	32.07	(2.62)	7	29.98	(2.13)	1.895	15	0.077
Thigh	10	25.48	(3.12)	8	23.80	(1.69)	1.334	14	0.204
Crus	8	24.63	(2.78)	8	22.28	(2.23)	1.873	14	0.082
Forelimb	8	67.09	(4.56)	8	63.13	(4.24)	1.889	16	0.077
Hindlimb	8	50.11	(5.82)	8	46.08	(3.72)	1.653	14	0.121
"Intermembral" index	8	136.99	(13.92)	8	137.50	(11.35)	-0.08	14	0.937
"Humerofemoral" index	8	133.51	(14.61)	8	131.77	(14.34)	0.241	14	0.813
"Brachial" index	10	109.47	(5.25)	7	115.03	(9.89)	1.507	15	0.153
"Crural" index	8	96.90	(4.18)	8	93.56	(5.73)	1.332	14	0.204

to adult females (e.g. Galdikas, 1985; Kingsley, 1988) however, the results here suggest their limb morphology is similar to that of flanged males. This is perhaps not altogether surprising since although unflanged males arrest their development (a likely consequence of the presence of other flanged males - Maggioncalda et al., 1999), after this period of arrest the development from unflanged to flanged is quite a rapid process, often within the space of a year (Harrison and Chivers, 2007). Whilst the possibility of a growth spurt in the skeletal system during transition for unflanged to flanged is not untenable, the results here suggest that bimaturism in orangutans is characterised by weight gain and the onset of secondary sexual characteristics such as cheek flanges, throat sacs, long hair and vocalizations, rather than skeletal growth. Thorpe and Crompton (2005) found that flanged and unflanged males were similar in their locomotor behaviour in Sumatran dry forest. However, for Bornean orangutans,

unflanged males were found to be more similar to adolescents, most likely reflecting the propensity for flanged males to travel on the ground and at lower levels in Borneo (MacKinnon, 1974; Galdikas, 1979; Rodman, 1979a; Tuttle, 1986, chapter 2), rather than size related differences. It has been suggested that sexual dimorphism in orangutans is a result of indeterminate growth by males, and this pattern of weight gain without skeletal growth may in part explain the tendency for flanged males to become obese in captivity (Leigh, 1992; Leigh and Shea, 1995).

The weights of orangutans obtained in this study appear low compared to those documented in previous studies (Markham and Groves, 1990) and considering weights on captive animals (Loomis, 2003). However, captive orangutans are likely to be heavier given their high quality diet coupled with their susceptibility to becoming overweight in captivity. The orangutans from Nyaro Menteng were rescued and then translocated and therefore may have been slightly underweight as a consequence of poor quality diet at the time they were rescued, however, the upper-end weights correspond to those reported in Markham and Groves (1990). The body condition of the orangutans were recorded as predominantly "normal" (71.1%) or "thin" (22.2%), with only 6.7% of the sample being recorded as "fat".

Male orangutans are both larger and heavier than sexually active females and non-sexually active females, reflecting the pronounced sexual dimorphism in orangutans. Growth in female orangutans is considered to be a prolonged but determinate process, whereas in male orangutans growth is though to be continuous, and it is this process that is responsible

for the high degree of sexual dimorphism in orangutans (Leigh and Shea, 1995). It is estimated that the cessation of growth is around 18 years old in female orangutans (Leigh and Shea, 1995) and that wild female orangutans reach sexual maturity between 11 and 15 years old, although they may not breed until several years later than that (Galdikas, 1981; Leighton et al., 1994). This led us to predict that sexually active females would be larger than non-sexually active females. However, comparison of the measurements obtained from Nyaro Menteng between females indicates there is little difference between sexually active and non-sexually active females in terms of both body mass and limb length. Phillips (2011) found that orangutans reach full independence for locomotion at around 6 years of age in *P. p. wurmbii*, although this was found to be later (around 8 years) in less disturbed forest, for the same species (Bard, 1995). The limb lengths of younger females may therefore reach a similar size to fully mature females reasonably early in development in order to facilitate locomotor behaviours particularly with regard to the gap crossing capabilities which are fundamental to negotiating an arboreal environment.

When measurements were corrected for differences in body mass, whilst retaining size-related shape information, no differences were observed between the four age-sex classes considered in this study. This result confirms our prediction that orangutans are isometrically similar with males being essentially larger versions of females, or females being smaller versions of males. However, this is perhaps not altogether suprising as locomotion has been found to be similar between age-sex classes (Thorpe and Crompton, 2005; chapter 2; chapter 3) and therefore we would not really expect the locomotor anatomy to differ, regardless of sexual

dimorphism and bimaturism.

The average error in the branch measurements was less than 1% which indicates that measurements obtained from photographs using parallel lasers were accurate. Whilst the sample size for the laser measurements is small, since there is currently little information regarding the postcranial anatomy of orangutans, and particularly wild orangutans, the contribution of these measurements to the study of primate morphology is important.

The measurements taken using the parallel lasers did not uphold our hypothesis (3) that orangutans might be smaller in Borneo as a result of the lower quality diet. The Bornean sub-species (*P. p. wurmbii*) and Sumatran species (*P. abelii*) showed remarkable similarity in limb length and long bone indices. Recent studies have shown that age-sex class has only a limited influence on locomotor behaviour which reflects both the use of arboreal pathways in Sumatra and the homogeneous structure of logged peat swamp forest in Borneo (Thorpe and Crompton, 2005; chapter 2; chapter 3; chapter 4). A comparison of the trees used during travel in a Sumatran peat-swamp and a Bornean peat-swamp found that the mean gap size between trees was similar, in spite of variation in the overall structure of "travel trees" between sites. The ability to cross gaps in the canopy is paramount for efficient arboreal travel as it reduces path length, otherwise individuals may need to expend more energy by either travelling a longer distance around a gap, or descending to the ground and climbing again the other side (Temerin and Cant, 1983; Cant, 1988). This could suggest that the selection pressure for "optimal" lengths of fore and hindlimbs to facilitate locomotion in an arboreal environment, particularly for gap crossing

Table 5.8 – Percentages of commonly observed locomotor modes in four orangutan study sites

Mode	Submode	Ketambe[a]	Suaq Balimbing	Sabangau	Tuanan[b]
		(n = 1,783)	(n = 1,762)	(n = 2,037)	(n = 1,950)
Quadrupedal and Tripedal Walk		**17.6**	**10.8**	**8.5**	**7.4**
	Walk	8.0	5.2	4.2	6.0
	Pronograde Scramble	9.4	5.6	4.3	1.4
Torso-Orthograde Suspension		**35.0**	**40.4**	**47.9**	**34.8**
	Brachiation	6.2	7.6	4	3.1
	Forelimb Swing	8.4	6.2	2.9	2.3
	Orthograde Clamber	14.4	21.3	35.9	21.6
	Orthograde Transfer	6.1	4.8	5.0	7.9
Torso-Pronograde Suspension		**3.6**	**3.4**	**1.3**	**1.2**
	Inverted Pronograde Walk	2.3	2.8	0.4	0.8
	Inverted Pronograde Scramble	1.3	0.6	0.7	0.4
Forelimb-Hindlimb Swing		**0.3**	**2.0**	**1.0**	**0.1**
Bipedal Walk		**7.3**	**5.4**	**3.2**	**8.4**
	Bipedal Walk	1.6	0.6	0.1	0.8
	Assisted Bipedal Walk	5.6	4.8	3.2	7.6
Bridge		**2.8**	**1.9**	**1.9**	**4.0**
Vertical Climb		**16.0**	**13.3**	**9.8**	**10.5**
	Flexed-Elbow	5.6	9.0	6.4	8.4
	Extended-Elbow	1.2	0.5	0.8	0.0
	Vertical Scramble	7.1	2.0	0.8	2.1
Vertical Descent		**9.4**	**6.6**	**5.2**	**1.9**
Drop		**1.8**	**0.8**	**1.1**	**0.5**
Ride[c]		**0.5**	**0.6**	**0.8**	**30.4**
Sway[c]		**5.6**	**14.9**	**19.0**	**-**

[a] Data from Thorpe and Crompton (2006)
[b] Data from Phillips (unpublished data)
[c] Sway and Ride were combined for Tuanan due to methodological differences

behaviour, outweigh the energetic cost associated with maintaining large body size. However, since there are no known weights for wild Sumatran orangutans, there is a possibility that they have different body sizes as a consequence of of the disparity in diet, but have maintained limb length.

The musculature of the orangutan forelimb, particularly the elbow flexor muscles and muscles of the forearm, which allow a greater mobility of the wrist, are considered functional specialisations for arboreal locomotor behaviour, such as vertical climbing and orthograde suspensory locomotion (Payne et al., 2006b; Oishi et al., 2008, 2009). However, Myatt et al. (2011a, b) found that non-human apes did not vary significantly in the PCSA and fascicle length for the majority of muscle groups from either the fore or hindlimb, contradicting previous studies that suggest even small differences in the frequencies of locomotion are reflected in the macro-architecture of muscles (e.g. Fleagle and Meldrum, 1988; Ward and Sussman, 1979; Payne et al., 2006c; Oishi et al., 2008, 2009). Orangutans inhabit structurally different habitat types on both Borneo and Sumatra (chapter 4) however the locomotor repertoires of orangutans are essentially the same (Table 5.8) although the proportions of observed locomotor behaviours differ both between species and between habitat type (Thorpe and Crompton, 2006; chapter 4). Furthermore, both species have retained similar profiles in terms of preferred supports regardless of habitat type and associated forest structure (chapter 4). Thus we would expect their basic functional anatomy to remain similar and the results of this study do suggest that they are essentially similar in terms of their postcranial morphology.

5.5 Conclusions

Although flanged males are heavier than other age-sex classes, in terms of limb length unflanged males are of a similar size to flanged males indicating that transition to the flanged state is more associated with weight gain and the development of cheek flanges and throat pouches rather than skeletal growth. There is a disparity in size between males and females reflecting the sexual dimorphism of the genus, although males are essentially larger versions of females in terms of limb proportions.

No differences were observed for limb lengths or indices between *P. abelii* and *P. p. wurmbii* indicating that the poor quality of diet experienced on Borneo is not reflected in their body size. The selection for large body size with similar limb proportions is likely to facilitate successful arboreal locomotion, and particularly gap-crossing behaviour, in the structurally diverse forest types in which orangutans survive.

CHAPTER 6

Orangutan Locomotion: Influenced by habitat over inter-specific differences

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KLM collected and analysed the data and wrote the manuscript, SKST developed the methods and contributed to the writing of the manuscript

ABSTRACT

This is the first study to undertake a full comparison of interspecific differences in orangutan locomotion using rigorous statistical testing. We examined locomotor behaviour in three study sites in Indonesia, two on Sumatra (*Pongo abelii*): Ketambe (dry lowland forest) and Suaq Balimbing (peat-swamp forest); and one on Borneo (*Pongo pygmaeus wurmbii*): Sabangau (peat-swamp forest). Log-linear modelling was used to examine how the different species interacted with their environment in terms of the number, size and types of arboreal supports used during locomotion, and whether these differences were greater at the habitat or species level; or whether differences existed between all study sites. The results revealed that orangutan locomotion and support use was strongly influenced by habitat type. The strongest association was between habitat, support type and support diameter, incorporating information on the number of supports used for weight bearing, although this may merely signify differences in support availability between sites. Orangutans in dry lowland forest generally use larger branches and boughs for locomotion than in peat-swamp forest, whereas in peat-swamp forest orangutans use both single and multiple trunks and mixed supports more frequently. Log-linear modelling revealed that orangutan locomotion is best explained in simple terms based on the orientation of the torso, rather than differentiating between more distinct forms of locomotor behaviour, or in terms of suspensory or compressive locomotion. The results of this study indicate that similarities in orangutan locomotion are more important than differences imposed by forest structure as the association between locomotion and support characteristics was stronger than any influence of habitat type on orangutan locomotion.

6.1 Introduction

BOTH species diversity and habitat structure have the potential to cause variation in locomotor behaviour among arboreal primates. Until relatively recently orangutans were classified as one species comprising two subspecies, one on Sumatra and one on Borneo. However, current classifications recognise two separate species (Sumatran: *Pongo abelii* and Bornean: *Pongo pygmaeus*) with three subspecies of the Bornean orangutan (Zhi et al., 1996; Warren et al., 2001; Steiper, 2006; Goossens et al., 2009). There is much documented geographic variability between orangutan taxa which are considered to be a result of both phenotypic plasticity and genetic differences. For example, diet is to a large extent due to plastic responses to variation in food availability, and the varied response to logging between the two species suggests morphological and physical differences (see review in van Schaik et al., 2009). The two orangutan species show a large amount of genetic differentiation, which could potentially explain documented geographic variation in behaviour (Wich et al. 2009). However, genetic differences have recently been shown to explain very little of this variation whereas environmental variation explained much more, indicating that developmental plasticity has a large influence on orangutan behavioural ecology and social organisation (Krutzen et al., 2011).

Orangutans on both Borneo and Sumatra inhabit a wide range of habitats in primary and secondary forest types, with prime orangutan habitat being dry lowland forest and hill dipterocarp forest, freshwater swamp forest, peat-swamp forest in poorly drained river basins and alluvial forest in river valleys (Rodman and Mitani, 1987; Knott, 1999; Morrogh-Bernard et al., 2003; Husson et al., 2009), although orangutans also occur at very low

densities in other forest habitats, such as heath forest (*Kerangas*) and limestone-karst forest (Payne, 1988; Marshall et al., 2006, 2007). However, in both Borneo and Sumatra orangutans occur at their highest densities in mosaic sites, where individuals have access to two or more different types of habitat within their home ranges, rather than in single habitat types (Husson et al., 2009). This was attributed to the likelihood that whilst one habitat may be more productive overall, orangutans will be able to access neighbouring habitat which may have a more stable, year-round supply of food (Cannon et al., 2007; Husson et al., 2009).

Despite differences in brain size (Taylor, 2006; Taylor and van Schaik, 2007), craniofacial morphology (Groves and Shea, 1992; Taylor, 2006) and dental morphology (Uchida, 1998), which are considered to result from a disparity in the quality of diet between Borneo and Sumatra, no differences in postcranial morphology have yet been identified. Manduell (chapter 5) compared interspecific limb lengths but found little difference, suggesting that selection pressures on fore- and hindlimb lengths are similar on both islands, despite differences in habitat. However, limb lengths are only one component of an array of musculoskeletal variables that impact on locomotor behaviour. Other aspects of postcranial morphology, such as bone girth, joint surface size, muscle dimensions and muscle fibre types need to be assessed before we are able to fully understand the extent of inter-specific differences in the postcranial morphology of orangutan species and subspecies (Rodman, 1979b; Glassman, 1983). Previous studies have examined muscle groups but only on the Sumatran species (e.g. Myatt et al., 2011a, b). However, little difference was found in the muscle architecture (mass, PSCA, fascicle length) of the great apes therefore indicating their

generalist morphology and adaptation to orthogrady (Thorpe and Crompton, 2006; Crompton et al., 2008; Myatt et al., 2011a, b). It is therefore unlikely that any difference would be observed between the two orangutan species, given their similar behavioural repertoires. However, since comparative musculoskeletal data is extremely difficult to obtain, a useful first step in discovering whether postcranial diversity exists between species is to quantify whether the differences in locomotor profiles can be explained exclusively by habitat, or whether there are any differences left over that cannot be accounted for ecologically.

Locomotor behaviour is cognitively challenging, particularly for the orangutan given its large size and arboreal lifestyle (Chevalier-Skolnikoff et al., 1982; Povinelli and Cant, 1995; Hunt, 2004; Russon and Begun, 2004; Tecwyn et al., 2012). Several populations of Sumatran orangutans have been observed to use tools, whereas regular tool use that also involves tool manufacture is absent in Bornean populations (van Schaik, 2004; van Schaik et al., 2009). This difference may be a consequence of greater sociability in Sumatran populations, which affects the efficacy of social learning (Van Schaik et al., 2003, 2006; Russon et al., 2009; van Schaik et al., 2009), however, the larger brain size of Sumatran orangutans may also play a role (van Schaik et al., 2009). Thus there may be cognitive differences between orangutan taxa which might result in species differences in the solutions they find to problems associated with negotiating a complex habitat.

Given the broad repertoire of orangutan positional behaviour, with over 100 biomechanically distinct postural and locomotor modes (Thorpe and Crompton, 2006; Thorpe et al., 2009), we would expect orangutans to be able

to adapt to even subtle variations in forest structure by matching locomotor behaviour to the supports prevalent in the environment. This would reduce vertical and horizontal displacement during travel, thereby reducing path length and energy expenditure. This certainly appears to be the case since comparisons of wild orangutan locomotion have found that their overall repertoire is broadly similar (Appendix B). However, the homogeneous nature of disturbed peat-swamp appears to have limited the locomotor behaviour of orangutans to high frequencies of only a few behaviours (chapter 3, chapter 4). Orangutans in Sumatra were also found to exhibit higher frequencies of pronograde behaviour (arboreal quadrupedalism, pronograde suspensory locomotion and pronograde bridging), than observed in the Bornean species (Thorpe and Crompton, 2006; chapter 4). However, of the pronograde behaviours it is likely that pronograde bridging will place the anatomy under the most stresses as a result of its association with the most compliant supports (Thorpe et al., 2009). Since the musculoskeletal system must adapt not only to the most frequent behaviours but also to the most strenuous activities in which they are used, the selection for proficiency in pronograde bridging involves the use of the most compliant supports therefore must have influenced the evolution of orangutan morphology (Alexander, 1981; Thorpe et al., 2009). Thus, since pronograde bridging behaviour is an important adaptation for negotiating the terminal branches to cross tree crowns and was observed in both species, and at similar frequencies (chapter 4) it must have influenced orangutan morphology across taxa.

The degree of difference in the expressed positional behaviour of wild orangutans inhabiting different forest types is likely to depend on the extent

of variation of structural attributes such as support availability and the height and openness of the canopy, as these influence the strata in which orangutans travel, and the necessity for gap crossing behaviour. The locomotor behaviour of orangutans in Sumatran dry lowland forest was found to have strong associations with support type and diameter indicating they have evolved distinct modes to solve problems associated with living in a complex environment (Thorpe and Crompton, 2005). Therefore if the prevalence of supports of varying type and size were more limited, as is the case in peat-swamp forest (chapter 4), we would expect this to also limit the options for locomotor/support preferences. If habitat variation has a stronger influence on the locomotor behaviour of orangutans than inter-specific differences; this would lead us to predict that the locomotor behaviour of orangutans inhabiting the two peat-swamp forest sites would be more similar to each other than to those inhabiting dry lowland forest.

Few inter-specific studies of primate positional behaviour exist and most have been restricted to broad comparisons of frequencies obtained from different studies (e.g. Fleagle and Mittermeier, 1980; Cant, 1987a; Garber, 1991; Thorpe and Crompton, 2006; 2009) or have involved the use of a series of statistical tests to examine multidimensional relationships, which tend to be less robust (e.g. Hunt, 1992; Doran, 1993b; Dagosto, 1994; McGraw, 1996, 1998). This study is the first to combine data obtained with the same methodology from three orangutan study sites, and to employ multivariate statistical testing to compare both orangutan species in different forest types, thereby increasing our understanding of species and ecological diversity. We used a log-linear modelling approach, to examine the

association between orangutan locomotion and support characteristics (diameter, type and number of supports used), according to species, habitat type and study site. Whilst differences may occur between species and study site we predict that the greatest differences will be at the habitat level.

To this end, we compared data from the two study sites which represent good examples of the extremes of orangutan habitat type: Sabangau (disturbed peat-swamp forest, Central Kalimantan, Borneo, *P. p. wurmbii*) and Ketambe (mixed dry lowland forest, Leuser Ecosystem, Sumatra, *P. abelii*). We also obtained new locomotor behaviour data for orangutans at Suaq Balimbing, an undisturbed peat-swamp forest in the Leuser Ecosystem, Sumatra, since this allowed comparison of the relationship between forest type and locomotion within a single species (*P. abelii*).

6.2 Methods

Field Study

The study on the Bornean sub-species *Pongo pygmaeus wurmbii* was undertaken in the Sabangau research site between March and September 2007 and April 2009 and January 2010. The Sabangau research site is in the LAHG (Laboratorium Alam Hutan Gambut: Natural Laboratory for the Study of Peat-Swamp Forest; 2° 03′ S, 113° 54′ E), Central Kalimantan, Borneo. The site comprises peat-swamp forest around sea level. The study on the Sumatran species *Pongo abelii* was undertaken at two field sites in the Leuser Ecosystem, Aceh. Research was conducted in the peat-swamp forest of Suaq Balimbing between August 2010 and April 2011. Suaq Balimbing is situated in the western coastal plain of the Leuser Ecosystem, Sumatra (3°

42′ N, 97° 26′ E). We also incorporate Thorpe and Crompton's (2005) data on *P. abelii* from Ketambe which is predominantly primary mixed dry lowland forest situated in the northeast of the Leuser Ecosystem, Sumatra (3° 41′ N, 97° 39′ E), at an altitude of 350m upwards (Wich et al., 2009).

Orangutan positional behaviour observations in Ketambe were made by a single observer (SKT), and all observations in Suaq Balimbing and Sabangau were made by a single observer (KLM) during nest-to-nest follows of wild orangutans, following the same methods. Instantaneous samples on the 1-min mark were used to obtain detailed data of positional behaviour during nest-to-nest follows of wild orangutans. The methods have been described in detail elsewhere (Thorpe and Crompton, 2005; chapter 2; chapter 3). Details of data collected at each sample point are presented in Table 6.1.

For observations of locomotor behaviour, 1,762 observations were obtained from orangutans in Suaq Balimbing (see Appendix A, Table A.2 for details of study subjects); 2,037 in Sabangau (chapter 3) and 1,783 in Ketambe (Thorpe and Crompton, 2005).

Statistical Analysis

Backward elimination log-linear modelling is able to determine whether any significant relationships exist in multiway contingency tables and whether the distribution of the data can be explained by a simpler, underlying structure. It is suitable for categorical data and does not require the dataset to be normally distributed (Crook, 1997). In this study it was used to analyse multivariate relationships between locomotion; support type and support diameter (both of which incorporate information on the number of supports

Table 6.1 – Positional Behaviour Observations[a]

1. **Date**
2. **Individual**
3. **Time**
4. **Positional mode**[b]
   1. *Quadrupedal Walk:*
   2. *Bipedal Walk:*
   3. *Climb/descent*[c]*:*
   4. *Torso-orthograde suspension*[c]*:*
   5. *Torso-pronograde suspension*[d]*:*
   6. *Bridge*[d]*:*
   7. *Oscillation:*
5. **Height:** 5m intervals up to 30m, >30m (measured as the vertical distance from the animal to the ground).
6. **Number of Supports:** 1, 2, 3, 4, >4.
7. **Support Type:** Branch, bough, trunk, liana, other (aerial roots, nest).
8. **Support Diameter:** <2cm; ≥2 - <4cm; ≥4 - <10cm; ≥10 - <20cm; ≥20 - <40cm; ≥40cm.
9. **Behaviour:** Feeding (acquiring, processing, and eating); travelling.

[a] Data collection followed Thorpe and Crompton (2005)

[b] All follow those of Thorpe and Crompton (2006), which were based on Hunt et al. (1996). For detailed decriptions see Table 2.1, chapter 2

[c] For analysis, angled climb/descent was included with torso-orthograde suspensory locomotion following Thorpe and Crompton (2005).

[d] For analysis, pronograde suspension and bridge were conflated, as both had very small frequencies and are functionally similar.

used) with regard to field site (Site: Suaq; Sabangau; Ketambe), species (*P. abelii*; *P. p. wurmbii*) and forest type (Habitat: peat swamp forest; dry lowland forest), using SPSS version 19.0. Significant interactions can subsequently be ranked in order of relative importance (Crook, 1997). In log-linear analysis a significance value of 1 for the $\chi 2$ likelihood ratio indicates a perfect fit of the model's predicted cell counts to the observed cell counts, although a P value of >0.05 is considered significant (Thorpe and Crompton, 2005; Thorpe et al., 2007b). The model expressions produced by log-linear models can be analysed in more detail to explore the nature of associations through contingency tables containing row and column percentages together with standardised cell residuals (SCRs). Standardised cell residuals indicate by their sign whether an interaction is more (positive values) or less (negative values) common than predicted by the model and by their size, to what degree, figures ±2 indicate a substantial deviation from the model predictions, and consequently are of particular interest (Thorpe et al., 2007b). For more detailed information on this technique see Agresti (1990), Thorpe and Crompton (2005) and chapter 2.

Model Selection

In order to find the simplest way to classify the data and meet the assumptions required by log-linear analysis, i.e. no sampling zeros and no more than 20% of cells should have an expected value of less than 5; variables were conflated in various ways (Tabachnick and Fidell, 1996). Locomotor modes were conflated in terms of biomechanical similarities and support type and support diameter in a manner which incorporated the number of supports into the classification, for example, type: single branch/bough and multiple branch/bough since Thorpe and Crompton

(2005) found this to be the most meaningful way to model support use (for variable classifications see Table 2.2, page 47). Structural zeros (i.e. combinations which are not possible) that resulted from the incorporation of the number of supports within the support type and diameter variables and the incorporation of species and habitat type can be accounted for in the models. Models for all combination of variables were examined and then ranked in order of P-value.

6.3 Results

For all models locomotion was best classified in terms of the orientation of the torso, differentiating between pronograde locomotion, orthograde locomotion and oscillation, which includes tree-sway and is where supports are deflected simply with body weight or by oscillating supports with increasing magnitude to bridge a gap, and combines a combination of pronograde and orthograde body postures. Support type was best classified when tree trunks were conflated into the same category as lianas; and branches and boughs were combined in a separate category. Interestingly, this is effectively a proxy for support orientation rather than type, as trunks and lianas tend to be vertical whereas boughs and branches are angled or near horizontal. However, it must be noted that in peat-swamp the majority of locomotion on single and multiple trunks and/or lianas was locomotion on trunks, which accounted for 34.4% of all observations whereas locomotion on lianas accounted for only 2.9% of all observations. In contrast, locomotion on lianas accounted for 17% of observations in dry lowland forest, and locomotion on trunks only 4.7%. Support size was best explained in terms of a 4cm diameter threshold.

Table 6.2 – Log-linear models for the variables: species, habitat and study site

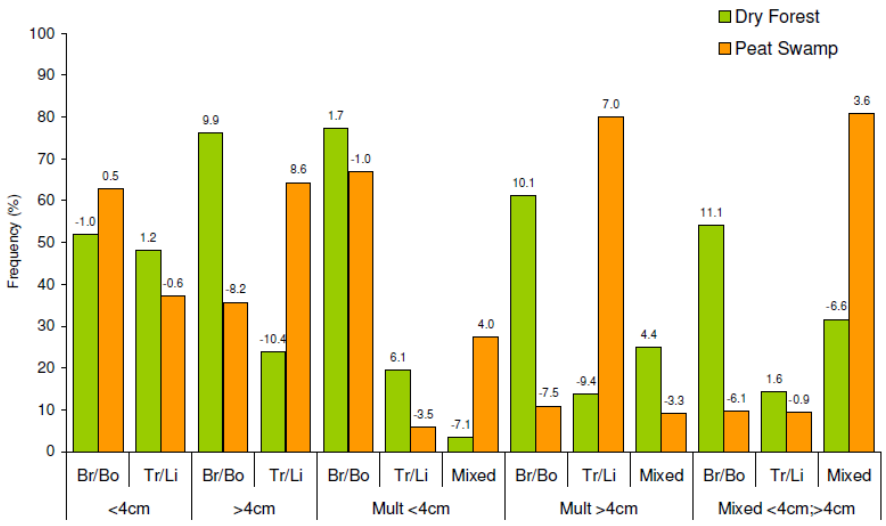
Model	Partial $\chi 2$	DF	P	Model Expressions	Standardised $\chi 2$ ($\chi 2$/DF)
LOCOj[a] * Type[b] * Diameter[c] * Habitat[d]	7.732	10	0.655	habitat * diameter * type	75.13
				locomotion * diameter * type	7.51
				habitat * locomotion * diameter	4.03
				habitat * locomotion * type	1.92
LOCOj * Type * Diameter * Site[e]	29.77	20	0.074	site * diameter * type	33.78
				locomotion * diameter * type	7.52
				site * locomotion * diameter	2.97
				site * locomotion * diameter	2.17
LOCOj * Type * Diameter * Species[f]	18.071	10	0.054	species * type * diameter	42.39
				locomotion * type * diameter	10.21
				species * locomotion * diameter	6.22
				species * locomotion * type	3.81

[a] LOCOj: Pronograde; Orthograde; Oscillation
[b] Type: Branch/Bough; Trunk/Liana; Multiple Branch/Bough; Multiple Trunk/Liana; Mixed
[c] Diameter: <4 cm; >4 cm; Multiple <4 cm; Multiple >4 cm; Mixed
[d] Habitat: Dry lowland forest; Peat-swamp forest
[e] Site: Ketambe; Suaq Balimbing; Sabangau
[f] Species: *P. abelii; P. p. wurmbii*

Table 6.2 shows that the habitat model was the best fitting model as it had a considerably higher P value than either the species or study site models. Nevertheless, all three models retained the same overall model expressions with the relationship between support diameter, support type and either habitat, site or species being the strongest in each of the models (Table 6.2). Within the model of best fit, support diameter and support type were conditionally dependent given habitat type and locomotor behaviour in the two most important model expressions. Thus the type and diameter of supports differed between the two habitat types, and the type and size of supports used varied according to locomotor behaviour. The relationship between locomotor behaviour and habitat type varied according to support diameter and support type respectively, and were the weakest associations in the model.

The association between habitat, support type and support diameter was the strongest variable interaction retained in the model, and was 10 times stronger than the next model expression (Standardized $\chi 2$ values, Table 6.2) indicating that support use by wild orangutans is most strongly influenced by habitat type. This relationship is detailed in Figure 6.1. Whilst the use of single supports (<4 cm) did not deviate from expected values in either dry lowland forest or peat-swamp forest (as indicated by the low SCRs), the use of single supports (>4 cm) did differ substantially between the two habitat types. Orangutans in peat swamp forest used single boughs/branches of >4 cm diameter much less than expected compared to orangutans in dry lowland forest, whereas they used single trunks or lianas of >4 cm more than expected, as indicated by contrasting SCR values (Figure 6.1). In dry lowland forest orangutans used multiple trunks/lianas (<4 cm) more than

Figure 6.1 – Model Interaction: Habitat * Type * Diameter



* *Figures are standardised cell residuals*

predicted, whereas orangutans in peat-swamp showed the opposite pattern. The use of mixed supports (<4 cm) were used much more than predicted by orangutans in peat-swamp forest, whereas these types of supports were used much less than predicted by orangutans in dry lowland forest.

There was also a large disparity between the two forest types in the use of multiple supports (>4 cm), with orangutans in dry lowland forest using both branches and boughs and mixed supports much more than expected as indicated by the high positive SCRs, whereas orangutans in peat-swamp only showed a strong positive association with multiple trunks and lianas (Figure 6.1). Orangutans in dry lowland forest used branches and boughs of mixed size (<4 cm; >4 cm) much more than predicted by the model, whereas in peat-swamp this was a strongly negative association. However, for mixed supports of mixed size, the opposite pattern was observed as there was a

much stronger association in peat-swamp than in dry lowland forest.

There is a distinct association between orangutan locomotion and support type and size, and this relationship is stronger than the influence of habitat on locomotion (Standardized $\chi 2$ values, Table 6.2). The relationship between locomotion, support size and support diameter, with corresponding SCR values is presented in Figure 6.2. Orthograde locomotion was dominant across all support type and diameter categories. Orangutans used single trunks/lianas (<4 cm) less then predicted for orthograde locomotion. Single trunks of both size categories were used more than predicted for oscillation, whereas single branches/boughs of both sizes were used less than predicted. Pronograde locomotion on single supports had a strong association with branches/boughs >4 cm, but took place much less than predicted on single trunks/lianas of the same size. For multiple branches/boughs <4 cm and mixed supports <4 cm, frequencies of observed behaviour did not substantially deviate from predicted values for either pronograde or orthograde behaviour, but there was a positive association with branches/boughs <4 cm and a negative association with mixed supports <4 cm for oscillation. Only orthograde locomotion had a positive association with trunks/lianas <4 cm, whereas this association was negative for pronograde behaviour and oscillation. For multiple supports >4 cm, pronograde locomotion had a strong association with branches/boughs but a negative association with trunks/lianas, whereas the opposite pattern was observed for orthograde locomotion. Only oscillation had a positive association with mixed supports >4 cm. Pronograde locomotion took place on branches/boughs of mixed diameter (<4 cm; >4 cm) more than predicted, but was observed less than predicted for other support types of

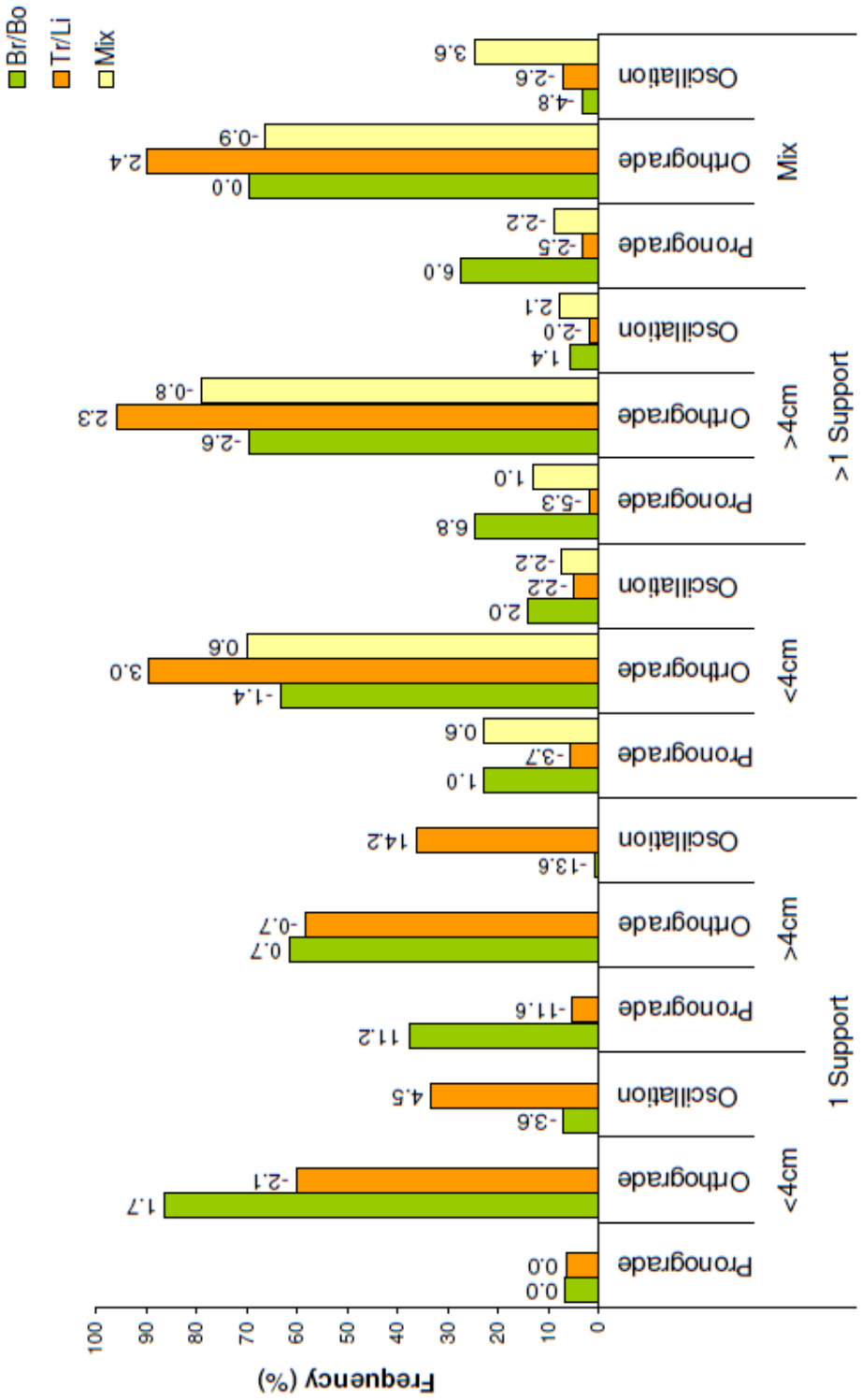
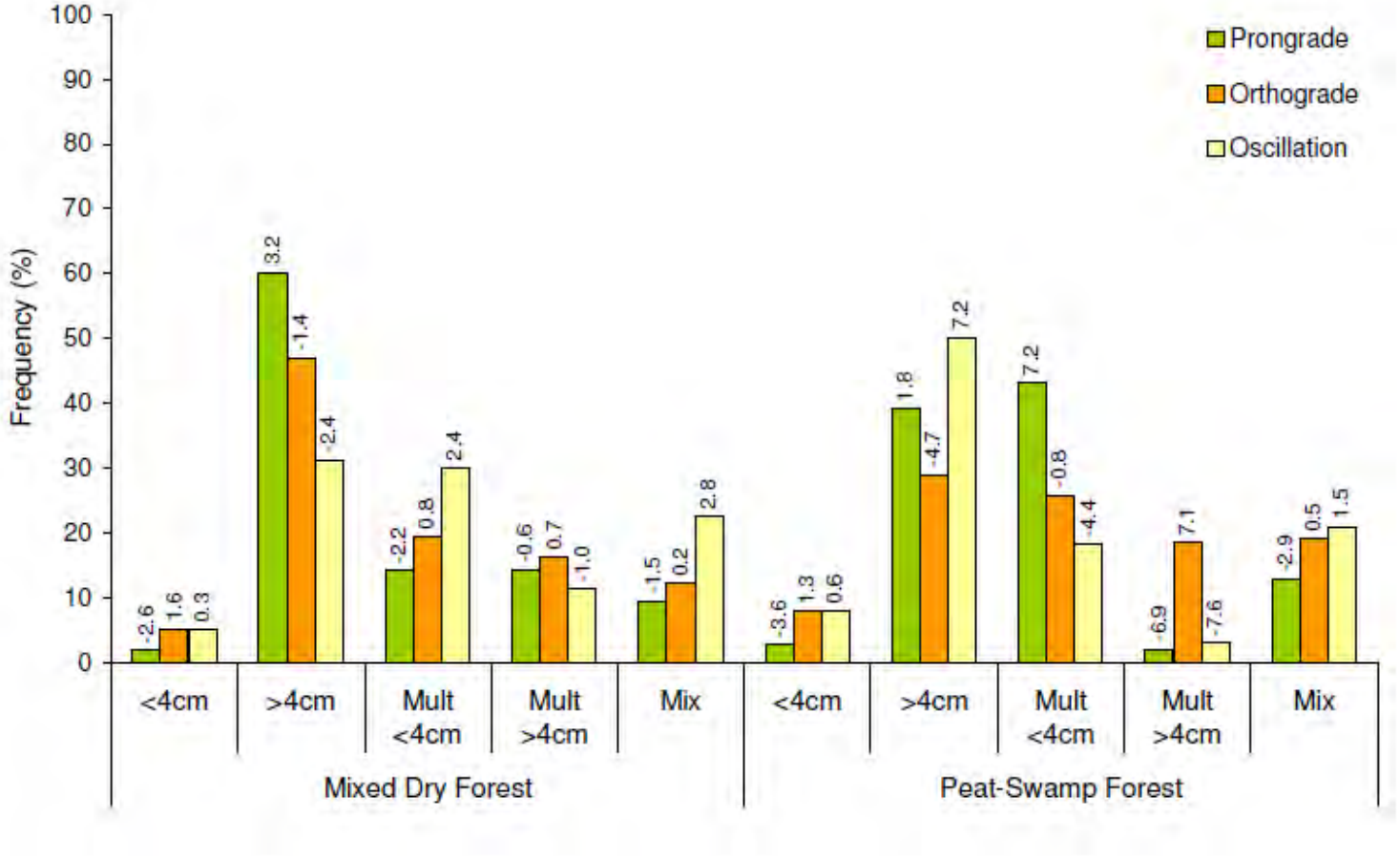


Figure 6.2 – Model Interaction: Locomotion * Type * Diameter

** Figures are standardised cell residuals*

Figure 6.3 – Model Interaction: Habitat * Locomotion * Diameter



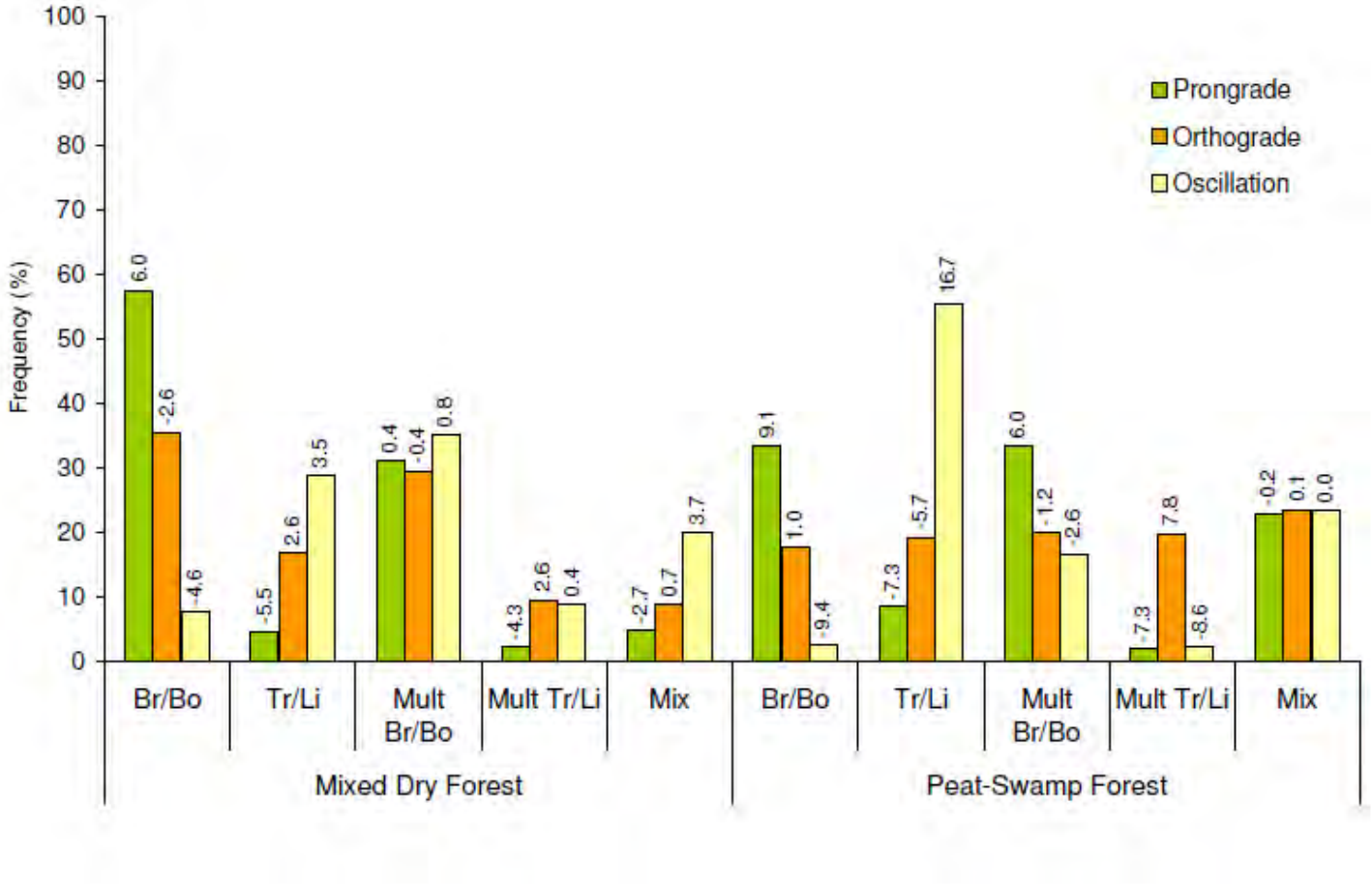
* *Figures are standardised cell residuals*

mixed size. Only orthograde locomotion had a positive association with trunks/lianas of mixed size, in fact, multiple trunks/lianas of all size classes had a negative association with all locomotor behaviour, with the exception of orthograde locomotion. Oscillation was the only locomotor behaviour to have a positive association with mixed supports of mixed size.

The association between habitat, locomotion and support diameter is presented in Figure 6.3. Locomotion on single small supports (<4 cm) had a similar pattern in both forest types (SCRs, Figure 6.3). Pronograde locomotion had a strong association with single large supports (>4 cm) in mixed dry lowland forest, whereas in peat-swamp forest it was oscillation that had the strongest association with this support size. The use of multiple small supports also differed between the two forest types, with pronograde locomotion having a strong association with supports of this size in peat-swamp but not in dry lowland forest. Furthermore, oscillation took place more than expected on multiple small supports in mixed dry lowland forest, but not in peat-swamp forest. The use of multiple supports (>4 cm) did not substantially deviate from expected values for all locomotor behaviour in mixed dry lowland forest, whereas in peat-swamp forest orthograde locomotion took place more than expected on supports of this size. Finally, orangutans in mixed dry lowland forest used supports of mixed size more than predicted for oscillation; but not for any other type of locomotor behaviour, this was not the case in peat-swamp where orangutans used mixed size supports similarly to those values predicted by the model, but did use them less than predicted for pronograde locomotion.

The association between habitat, locomotion and support type is presented

Figure 6.4 – Model Interaction: Habitat * Locomotion * Type



** Figures are standardised cell residuals*

in Figure 6.4. Single branches/boughs were used more than expected for pronograde locomotion but used less than expected for oscillation in both forest types (SCRs, Figure 6.4). Oscillation had a positive association with single trunk/lianas in both forest types, although orangutans in peat-swamp forest were twice as likely to use single trunk/lianas for oscillation as orangutans in mixed dry lowland forest. Single trunk/lianas had a negative association with orthograde locomotion in peat-swamp but not in mixed dry lowland forest. Pronograde locomotion had a negative association with single and multiple trunks and/or lianas in both forest types. In mixed dry lowland forest, multiple branches and boughs were used at a similar frequency for all locomotor behaviour, whereas in peat-swamp forest orangutans used multiple branches/boughs more than expected for pronograde locomotion, and less than expected for oscillation. Multiple trunks and lianas were used more than expected for orthograde locomotion in both forest types, but were negatively associated with oscillation in peat-swamp forest. Mixed supports were used with much higher frequency in peat-swamp forest than mixed dry lowland forest for all types of locomotion, although they were strongly associated with oscillation in mixed dry lowland forest.

6.4 Discussion

The results of this study imply that differences in support use during locomotor behaviour are a consequence of forest structure, since habitat produced a substantially stronger model than either species or study site. This supports our prediction that habitat would have more of an influence on locomotor behaviour than either species or study site. The strong association between habitat type and support characteristics (i.e. size and

type) indicates that support use by orangutans is strongly influenced by habitat type, however, this may merely be a consequence of support availability. In chapter 4 we found that orangutans across different forest types actively selected larger branches and boughs. Therefore, the higher frequency in use of larger branches in dry lowland forest compared to peat-swamp likely reflects the fact that there were more larger branches and boughs available. What is perhaps more interesting is that orangutan locomotion had a stronger association with support characteristics than any influence of habitat, suggesting that orangutan locomotion has evolved to be so plastic that despite even fundamental structural habitat differences, locomotor behaviour doesn't really differ.

The orientation of the torso as well as whether an animal is in suspension or compression, the direction of movement and which limbs are used for locomotion have been highlighted as important factors in order to match patterns of musculoskeletal action (Cant, 1987b; Hunt et al., 1996). In disturbed peat-swamp forest in Borneo, orangutan locomotion was best described simply in terms of suspensory and compressive locomotion (chapter 2, chapter 3), whereas in Thorpe and Crompton's (2005) study of orangutans in dry lowland forest, the locomotion variable combination retained much more detail and was described in terms of quadrupedalism, orthograde suspension, pronograde suspension, oscillation and vertical climb/descent. However, combining the data from the above two studies and incorporating new data from Suaq Balimbing, locomotion was best described very simply, in only three categories, based on the orientation of the torso. Interestingly, these combinations performed reasonably well in both Thorpe and Crompton's (2005) study in dry lowland forest in Sumatra,

as well as in disturbed peat-swamp forest in Borneo (chapter 2, chapter 3). We might have expected the difference between suspensory and compressive locomotion to be more important when comparing habitat type, with orangutans in more stunted peat-swamp forest being forced to exhibit more suspensory behaviour on multiple supports, whereas orangutans in dry lowland forest, where there is a higher prevalence of stiffer supports, might have been expected to exhibit higher frequencies of the more energetically efficient compressive locomotion, but this was certainly not the case. Therefore, although suspensory behaviour increases safety (Cartmill, 1985a), it is actually the orientation of the torso which enables orangutans to solve problems with negotiating a complex environment.

The way in which support type was conflated reflected the general orientation of supports, with trunks and lianas being typically vertical in orientation and branches and boughs being angled or horizontal. Cant (1987b) recognised the importance of support orientation for orangutan locomotion and noted that the high frequency of travel in the understory was facilitated by their ability to clamber across closely spaced lianas. More recently it was found that whilst support orientation did not directly influence locomotor behaviour in orangutans inhabiting dry lowland forest, it did influence the mean compliance of supports used (Thorpe et al., 2009). That support orientation, as a proxy for support type, was found to be important here contributes substantially to our understanding of orangutan locomotor behaviour.

Orthograde locomotion was the most commonly exhibited behaviour across

all support type categories, which we would expect since all apes are arboreally orthograde. However, orthograde locomotion was particularly associated with multiple trunks and lianas (i.e. vertical supports), and this trend was observed in both forest types (Figure 6.3) as well as in Cant's (1987b) study on the Bornean subspecies *Pongo pygmaeus morio* in dry lowland forest. Previous studies have suggested that in peat-swamp forest, where there is a lower density of lianas when compared to dry lowland forest, the closely spaced trunks of smaller trees may provide a similar functional role to that provided by lianas in dry lowland forest (chapter 3) and the results here seem to indicate that the presence of closely spaced vertical supports is an important aspect of traversing the arboreal environment for all orangutans, regardless of forest type. However, there were some notable differences between forest types in the use of support types during orthograde locomotion. Orangutans in dry lowland forest employed orthograde bahaviour on single trunks and lianas, which was not the case in peat-swamp forest. In contrast, orangutans in peat-swamp used multiple supports (>4 cm) during orthograde locomotion, reflecting the high frequency of the use of multiple tree trunks during orthograde clamber.

Whilst orthograde locomotion had a strong association with vertical supports, in contrast, pronograde behaviour tended to be associated with branches and/or boughs (i.e. horizontal or angled supports). Generally, orangutans used either single or multiple branches or boughs of the largest, or mixed sized categories. However, there were some differences in how orangutans used supports for pronograde locomotion between the two forest types. In dry lowland forest, orangutans used single supports >4 cm diameter, at much higher frequency than any other support diameter,

conversely, orangutans in peat-swamps used single >4 cm supports and multiple <4 cm supports at similar levels. We know from chapter 4 that orangutans actively select large branches and boughs for locomotion, therefore, the higher abundance of supports of this size in dry lowland forest compared to peat-swamp may facilitate locomotion on larger, stiffer supports. We would certainly expect orangutans to walk along the stiffest branches wherever possible in order to minimize energy expenditure on locomotion (Rosenberger and Strier, 1989; Strier, 1991; Warren and Crompton, 1998). However, orangutans use the compliance of supports to reduce energy expenditure during locomotion by swaying supports with increasing magnitude to bridge gaps in the canopy (Thorpe et al., 2007b). Pronograde locomotion, such as pronograde bridging and pronograde scrambling have been identified as key behaviours which enable orangutans to negotiate the smallest, most compliant supports, thus in peat-swamp forest, orangutans may be required to negotiate smaller, compliant supports more frequently than in dry lowland forest as a result of the more stunted forest structure, with reduced availability of large branches.

Oscillation is heavily reliant on compliant supports and is therefore restricted to smaller supports, the results of this study show that across forest types, single vertical supports (i.e. trunks and lianas) play an important role in facilitating this type of locomotion, as do mixed supports (i.e. trunks in association with a bough or branch). However, there are some differences between forest types in how orangutans oscillate supports, particularly for multiple branches/boughs, which were used at much higher frequency in dry lowland forest compared to peat-swamps. Orangutans in both peat-swamp sites frequently swayed trees about the

trunk using body mass alone, whereas in dry lowland forest orangutans were required to distribute their body weight over multiple supports in order to gain the required magnitude to bridge a gap. Indeed, orangutans were observed to oscillate part of large tree crowns in Ketambe using multiple branches in order to bridge gaps both within and between tree crowns (Manduell, personal observations). The incidence of tree-sway is much higher in peat-swamp than observed in dry lowland forest. This indicates that our suggestion in chapter 2, whereby orangutans in disturbed forest reduce the energetic cost of locomotion by loading smaller trunks with their body mass, causing them to deflect in one direction, is not limited to disturbed forest, as a high frequency of tree-sway using this technique was also observed in undisturbed peat-swamp (Suaq Balimbing). Orangutans in dry lowland forest (Ketambe) travelled at higher levels, thereby limiting access to the smaller more compliant trees, and smaller trees were less abundant in Ketambe than in the peat-swamp forests (chapter 4). Indeed, at higher levels of the forest canopy, lianas would more likely facilitate oscillatory locomotion, hence the stronger association with lianas for tree-sway in Ketambe (Thorpe and Crompton, 2005).

Whilst orangutan locomotion is certainly versatile and not restricted to specific locomotor/support preferences, the results of this study have identified certain trends with regard to the orientation of the body. The results of this study are particularly interesting given theoretical predictions that suggest suspensory postures should increase with increased body mass (Cartmill and Milton, 1977) and that orthograde suspension is considered to be a primary mechanism to enable large-bodied apes to solve problems in negotiating small peripheral branches (Grand, 1972; Cartmill, 1985a; Cant,

1992). However, recent studies of orangutan positional behaviour have found that hand-assisted bipedalism which is an orthograde compressive behaviour (Thorpe et al., 2007b); pronograde bridging which is a mixture of compressive and suspensory behaviour (Thorpe et al., 2009) and pronograde suspensory posture during feeding in the terminal branch niche (Myatt and Thorpe, 2011) are used to solve problems associated with small, compliant supports, rather than orthograde suspension, highlighting the plasticity of orangutan locomotor behaviour when negotiating small, compliant supports. The results of this study further our understanding of how orangutans interact with their environment and how adaptable they are to differences in forest structure, which is important since their habitat is becoming increasingly altered through anthropogenic disturbance. The results of this study can also have beneficial implications for both captive and rehabilitant orangutans by providing more appropriate environments, as a result of an improved understanding of their habitat requirements.

6.5 Conclusions

Log-linear analysis showed that habitat variation has a stronger influence on orangutan locomotor repertoire than either species or individual study site. Log-linear modelling also revealed that overall orangutan locomotion was best explained in terms of the orientation of the torso, rather than in terms of compressive or suspensory behaviour, suggesting that in terms of support use, the orientation of the body enables orangutans to solve problems associated with living in a complex environment. This is interesting as whilst orthograde behaviour dominates orangutan locomotion, it is pronograde behaviour, specifically bridging and suspension, both of which are rare or non-existent in other great apes, which

enable orangutans to negotiate the smallest most compliant supports, thus highlighting specialisations for arboreal locomotion. Support type and diameter, incorporating the number of weight bearing supports, had the strongest association with habitat, indicating that the prevalence of preferred supports strongly effects how orangutans interact with their environment. Orangutan locomotion had a stronger association with support characteristics than any influence of habitat, which indicates that the commonalities of orangutan locomotor behaviour are more important than any differences imposed by forest structure and the associated distribution and abundance of supports of differing sizes and types.

CHAPTER 7

Orangutans in peat-swamp forest use more compliant supports for locomotion than in dry forest

Kirsten L Manduell and Susannah K S Thorpe

KLM collected and analysed the data and wrote the manuscript, SKST developed the methods and contributed to the writing of the manuscript

ABSTRACT

Negotiating the small peripheral branches associated with crossing tree crowns is potentially problematic for large-bodied orangutans. We investigated the relationship between orangutan locomotion, support compliance (as estimated from stiffness score), and associated ecological variables by comparing the compliance of supports used by Sumatran orangutans (*Pongo abelii*) in two distinct forest types: dry lowland forest and peat-swamp forest, to discover whether habitat type significantly affects the dynamic between locomotion and support compliance. Overall, orangutans in peat-swamp forest used more compliant supports than in dry lowland forest. Pronograde bridge took place on the most compliant supports in both forest types although these were more compliant in peat-swamp forest. This further demonstrates that orangutans deal with the most compliant supports through distributing their weight over multiple supports with a combination of both orthograde and pronograde postures, both in compression and suspension (Thorpe et al., 2009). Orangutans used stiffer supports when travelling higher in the canopy in order to increase safety. In peat-swamp, the larger-bodied flanged males used the stiffest supports indicating that when dealing with smaller, more compliant supports, body mass plays a more important role in support selection. Orangutans in dry lowland forest use much stiffer branches and boughs than in peat-swamp. However, the most compliant supports used in both forest types were those of mixed angle indicating that orangutans are able to deal with support compliance by distributing their weight over supports of different orientation, which may help counter the effect of compliance in each individual support.

7.1 Introduction

THE arboreal environment is a complex array of supports varying in size, type, strength, orientation and flexibility and arboreal primates must negotiate this continually changing environment to travel between food patches. Cant (1992) identified the ability to negotiate large supports as a fundamental habitat-related problem that arboreal primates must deal with to solve energetic challenges associated with locomotion in the canopy. However, the ability to deal with the compliant or flexible supports, against which animals must exert force in order to propel themselves through the canopy's diverse network, is also a particular problem for large-bodied arboreal primates (Thorpe et al., 2007b; 2009). Tree branches are tapered and distally become smaller, weaker and less stable (Grand, 1972; Cant, 1992). Since gaps in the canopy are typically crossed via tree crowns (rather than via the ground), the problem of crossing between trees is further exacerbated by the fact that under the mass of an animal thin peripheral branches deflect considerably, thereby increasing the effective gap size. Thus, the ability to deal with compliant supports effectively is crucial to efficient travel in an arboreal environment.

The elastic properties of supports may nevertheless be beneficial as well as costly to arboreal primates, depending on their mass and morphology (Alexander, 1991; Günther et al., 1991; Crompton et al., 1993). Cant (1994) noted that the smallest primates are able, by virtue of their small mass, to ignore compliance as even the smallest supports remain relatively stiff under their weight. However, support compliance is not always beneficial as the likelihood of supports bending and breaking increases with increased body mass (Cartmill, 1985a; Povinelli and Cant, 1995) and medium sized

primates must adjust for compliance, by waiting for a support to stop oscillating before proceeding, resulting in a loss of momentum and travel time (Cant, 1988). Indeed, flexible branches have been shown to increase the energetic cost of locomotion in both monkeys and lemurs (Alexander, 1992; Demes et al., 1995). Nevertheless, medium sized primates may be able to utilise compliant supports to aid leaping by actively pumping supports before take off (Cant, 1994). For large bodied primates, orangutans are notable in their ability to utilize the elastic energy stored in supports during tree-sway whereby they use their large body mass to oscillate a support with increasing magnitude in order to reach across a gap (Chevalier-Skolnikoff et al., 1982). In a study by Thorpe et al. (2007a) in which orangutan (*Pongo abelii*) energy costs were quantified, orangutans used substrate compliance to decrease the energetic cost of locomotion by tree-swaying, which was found to be less than half as energetically costly as jumping and an order of magnitude less costly than descending the tree and climbing again on the other side of the gap. In addition to utilising compliant supports for gap crossing via tree-sway, orangutans have also been found to use unique strategies to cope with the smallest, most compliant supports; such as a mixture of orthograde and pronograde behaviour together with a slow and irregular gait on multiple supports (Thorpe et al., 2009), which lowers peak forces on any single support and enhances stability.

For orangutans, accessing the terminal branch niche for both foraging and crossing via tree crowns is expected to be particularly problematic given their large body size (Myatt and Thorpe, 2011). Orangutans show extreme sexual dimorphism and bimaturism, flanged males weigh approximately

1.5 times more than unflanged males and more than twice as much as adult females and non-sexually active females (chapter 5). This large difference in body mass between age-sex classes should suggest that adolescents and adult females are able to use more compliant branches than unflanged males, which in turn should be able to use more compliant supports than flanged males. Whilst this was found to be the case with regard to postural feeding behaviour (Myatt and Thorpe, 2011), for locomotion it was adult females which used the stiffest supports (Thorpe et al., 2009) and this was attributed to their propensity towards more conservative locomotor behaviour (Thorpe and Crompton, 2005; Thorpe et al., 2009). However, in Sumatra orangutans are known to use arboreal pathways common to all individuals in a population (MacKinnon, 1974; Cant, 1992; Thorpe and Crompton, 2005; chapter 4), which may suggest there will be little differences in the type and size of supports used for locomotion between age-sex classes. There will undoubtedly be a threshold below which a support becomes too compliant for safe travel and Thorpe et al. (2009) suggested that orangutans will use locomotion/support combinations close to these thresholds in order to minimise the energetic cost of travel.

Previous studies investigating the affects of support compliance on orangutan positional behaviour were undertaken in dry lowland forest (Thorpe et al., 2007a, 2009; Myatt and Thorpe, 2011), which has wider variation in the type and size of available weight-bearing supports than peat-swamp forest (chapter 4). In chapter 6, we found that habitat had a strong influence on orangutan locomotion, in terms of the type and size of supports used. In addition, Sumatran orangutans inhabiting peat-swamp forest were found to use smaller supports more frequently than observed

elsewhere (chapter 4). Whether orangutans in Sumatran peat-swamp forest (which has a reduced abundance of larger supports and a more open canopy than dry lowland forest) will use more compliant supports for locomotion is currently unknown. We might expect little difference in the threshold of support compliance, below which it is unsafe for travel, given constraints imposed by body mass. However, the more open canopy of Sumatran peat-swamp forest (chapter 4) may force orangutans to negotiate the terminal branch niche typified by small, compliant, peripheral supports to transfer between tree crowns and therefore the threshold may be lower than predicted in Thorpe et al.'s (2009) study in dry lowland forest, where by virtue of their environment, they have access to larger supports.

Safety is of fundamental importance to arboreal primates and the risk of falling from a great height is of greater risk for large animals, such as the orangutan (Pontzer and Wrangham, 2004; Thorpe and Crompton, 2009; Thorpe et al., 2009). Whilst the locomotor behaviour of orangutans is likely to be a balance between both safety and the energetic cost of travel, we would expect that when travelling higher in the canopy, orangutans in all habitat types will select more stable supports in order to increase safety and reduce the increased risk of injury from falls. This was observed in both dry lowland forest in Sumatra (Thorpe et al., 2009), and in disturbed peat-swamp forest in Borneo (chapter 3).

Since, in chapter 6, we found that orangutan locomotion was strongly influenced by habitat type, we expand on a previous study of orangutan locomotion and support compliance in dry lowland forest (Thorpe et al., 2009) by examining the strategies orangutans in Sumatran peat-swamp

employ to control support flexibility, and comparing these to orangutans in Sumatran dry lowland forest. In order to compare support compliance in the two forest types we used a stiffness score (SS), a measure of the mean diameter used for each bout in which up to four supports were used, based on the methods of Thorpe et al. (2009). We hypothesize (1) that orangutans in peat-swamp forest will use more compliant supports during locomotion than in dry lowland forest (Thorpe et al., 2009), since orangutan locomotion is influenced by habitat (chapter 6) and there is a more open canopy in Sumatran peat-swamp forest (chapter 4), which will reduce the level of overlap between tree crowns, coupled with the increase in effective gap size when the flexible branches are loaded with the mass of the orangutan; (2) orangutans in peat-swamp forest will also select stiffer supports when travelling at higher levels in the canopy in order to increase safety as was observed in dry lowland forest (Thorpe et al., 2009); (3) there will be little difference in the stiffness score between age-sex classes, given the presence of arboreal pathways, which all individuals follow (chapter 4), but adult females in Sumatran peat-swamp forest may use stiffer supports than other age-sex classes given their tendency towards more conservative locomotor behaviour, as observed in previous studies (Thorpe and Crompton, 2005; Thorpe et al., 2009; chapter 4); (4) a different relationship between support compliance and the type of supports used will exist between dry lowland forest and peat-swamp forest, given the increased use of tree trunks observed in peat-swamp forest, coupled with the reduced abundance of larger branches and boughs (chapter 4) and finally; (5) there will be a different relationship between support compliance and support angle, between the two forest types since in chapter 6, support type was found to be effectively a proxy for support angle, and orangutans in peat-swamp use

more vertical tree trunks during locomotion, whereas orangutans in dry lowland forest use larger branches and boughs (i.e. horizontal and angled) more often.

7.2 Methods

Field Study

This study was conducted between between August 2010 and April 2011. Suaq Balimbing is situated in the western coastal plain of the Leuser Ecosystem, Sumatra (3° 42′ N, 97° 26′ E), at around sea level the site mainly comprises peat-swamp forest whose peat layer increases in thickness away from the river and is home to the Sumatran orangutan species *Pongo abelii* (Wich et al., 2009). We also incorporate (Thorpe and Crompton's 2005) data from Ketambe, also home to the Sumatran orangutan species *Pongo abelii*, the site is predominantly primary mixed dry lowland forest situated in the northeast of the Leuser Ecosystem, Sumatra (3° 41′ N, 97° 39′ E), at an altitude of 350m upwards (Wich et al., 2009).

All observations in Suaq Balimbing were made by a single observer (KLM) during nest-to-nest follows of wild orangutans, all observations in Ketambe were made by another observer (SKT). Instantaneous samples on the 1-min mark were used to obtain detailed data of positional behavior during nest-to-nest follows of wild orangutans. The methods have been described in detail elsewhere (Thorpe and Crompton, 2005, chapter 2, chapter 3). A period of self-training in the estimation of height and diameter was carried out prior to data collection, and throughout the data collection period in order to maintain accuracy. Details of data collected at each sample point

are presented in Table 7.1.

For observations of locomotor behavior, 1,762 observations were obtained from orangutans in Suaq Balimbing, and 1,783 in Ketambe (Thorpe and Crompton, 2005). In Suaq Balimbing, thirteen individuals were followed, including all age-sex classes (Appendix A, Table A.2). Four age-sex classes were used, 14.2% of all observations sampled behavior of flanged males (3 individuals), 24.4% sampled adult females (4 individuals), 26.7 sampled unflanged males (3 individuals) and 34.7% sampled adolescents (3 individuals).

Statistical Analysis

To provide a measure of the compliance of supports used during locomotion, the continuous response variable, a stiffness score (SS; Thorpe et al., 2009; Myatt and Thorpe, 2011) was calculated for each observation. This is based on support diameter and the number of weight bearing supports (up to a maximum of four supports) for each observation following Thorpe et al. (2009). This stiffness score allows for the quantification of broad relationships between positional modes and the compliance of the supports on which they were exhibited. The SS is transformed using a natural logarithm (ln) giving a variable ln(SS) which, in the General Linear Models (GLMs) produced standardised residuals with an approximately normal distribution.

General Linear Models (type III hypotheses) using the natural log of the compliance score ln(SS) as the response variable are used to quantify the effect of support compliance on orangutan locomotion in the two forest

Table 7.1 – Positional Behavior Observations

1. **Date**
2. **Individual**
3. **Time**
4. **Positional mode**[b]
   1. *Quadrupedal Walk:*
   2. *Bipedal Walk:*
   3. *Climb/descent*[c]*:*
   4. *Torso-orthograde suspension*[c]*:*
   5. *Torso-pronograde suspension*[d]*:*
   6. *Bridge*[d]*:*
   7. *Oscillation:*
5. **Height:** 5m intervals up to 30m, >30m (measured as the vertical distance from the animal to the ground).
6. **Number of Supports:** 1, 2, 3, 4, >4.
7. **Support Type:** Branch, bough, trunk, liana, other (aerial roots, nest).
8. **Support Diameter:** <2cm; ≥2 - <4cm; ≥4 - <10cm; ≥10 - <20cm; ≥20 - <40cm; ≥40cm.
9. **Behaviour:** Feeding (acquiring, processing, and eating); travelling.

[a] Data collection followed Thorpe and Crompton (2005)

[b] All follow those of Thorpe and Crompton (2006), which were based on Hunt et al. (1996). For detailed decriptions see Table 2.1, chapter 2

[c] For analysis, angled climb/descent was included with torso-orthograde suspensory locomotion following Thorpe and Crompton (2005).

[d] For analysis, pronograde suspension and bridge were conflated, as both had very small frequencies and are functionally similar.

types. The effect of age-sex, height in the canopy, behavior, support type, support angle, number of weight bearing supports and locomotion on ln(SS) was tested. In addition, the effect of two-way interactions between forest type and each variable on ln(SS) was also tested in the models. Interaction terms increase the complexity of the model. The contribution of each interaction on the complexity of the model was quantified using the modified F-statistic on the error mean squares for alternate models. The significant differences between ln(SS) and each variable retained in the model were tested using Tukey's test of multiple pairwise comparison ($P<0.05$).

7.3 Results

The final GLM, showing the significant main effects and interactions, is presented in Table 7.2. Of the variables tested, all were found to be significant main effects with the exception of behavior (feeding or travelling). The final model also retained the interaction terms habitat * locomotion, habitat * age-sex, habitat * support type, habitat * support angle, and habitat * height in the canopy. The interaction term habitat * number of supports was not significant. The significant differences between ln(SS) within each of the main effects retained in the model are presented in Figure 7.1. These results show that bridging involved significantly more compliant supports than any other type of observed locomotor behavior (Figure 7.1a), followed by tree-sway, which is reliant on the compliance of supports, although the the mean SS for tree-sway was not significantly different than for orthograde suspensory locomotion. Quadrupedalism and vertical climb/descent were exhibited on the stiffest supports (Figure 7.1a). Overall there was an increase in the stiffness of supports used with

Table 7.2 – General Linear Model for Dependent Variable: Natural Logarithm of Stiffness Score

Source	Type III sum of squares	Degrees of freedom	Mean square	F	Significance
Corrected Model	1,398.894[a]	36	38.858	88.142	0.000
Intercept	1,860.567	1	1,860.567	4,220.336	0.000
Angle	5.723	3	1.908	4.327	0.005
Support type	178.385	4	44.596	101.158	0.000
Height	50.227	2	25.114	56.965	0.000
No. of supports	163.958	1	163.958	371.908	0.000
Age-sex class	32.241	2	16.120	36.566	0.000
Locomotion	134.672	6	22.445	50.913	0.000
Habitat	5.854	1	5.854	13.278	0.000
Habitat * Locomotion	6.286	6	1.048	2.376	0.027
Habitat * Age-sex	11.392	2	5.696	12.921	0.000
Habitat * Height	3.921	2	1.960	4.447	0.012
Habitat * Support type	24.222	4	6.055	13.735	0.000
Habitat * Angle	5.469	3	1.823	4.135	0.006
Error	1,337.121	3033	0.441		
Total	13,882.506	3070			
Corrected Total	2736.015	3069			

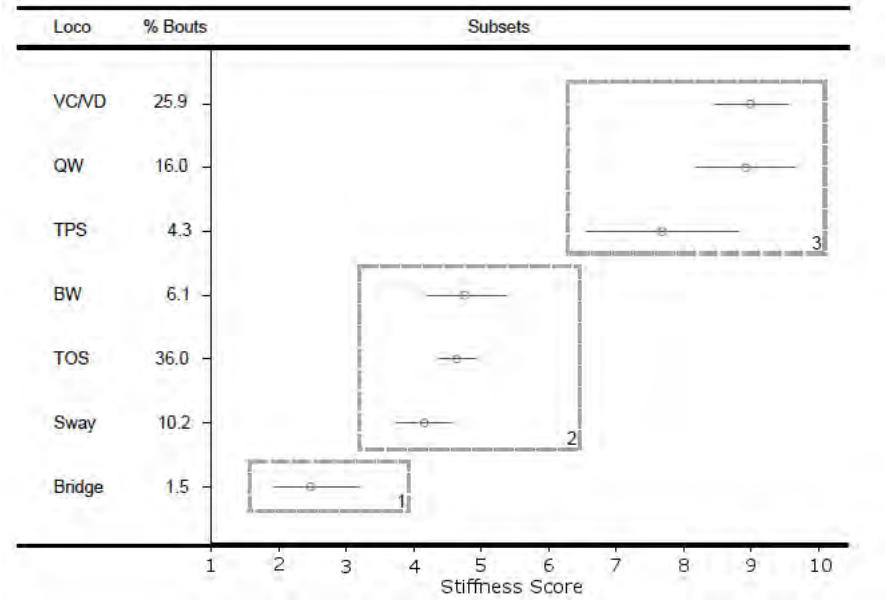
[a] $R^2 = 0.511$ (adjusted $R^2 = 0.505$).

increasing body size Figure 7.1b. with flanged males using significantly stiffer supports than other age-sex classes. Orangutans used increasingly stiffer supports with increased height in the canopy, with locomotion at heights above 20 m relying on the stiffest supports (Figure 7.1c). Tree trunks were the stiffest support type used during locomotion, whereas locomotion on the most compliant supports involved the use of combined tree supports (i.e. trunk/branch/bough) with a liana (Figure 7.1d). Angled supports were found to have the greatest mean stiffness with supports of mixed orientations having the lowest mean stiffness score (Figure 7.1e).

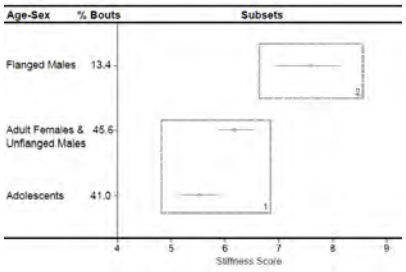
The interaction between habitat and locomotion shows that, overall, locomotion in peat-swamp forest used more compliant supports than in mixed dry forest (Figure 7.2). Bridging locomotion in peat-swamp forest used supports with a significantly lower mean SS than any other locomotor behavior, including bridging locomotion in mixed dry forest, which had the lowest SS for locomotion in dry forest. Sway took place on more compliant supports in peat-swamp than in mixed dry forest although the difference was not statistically significant as both form part of subset 2 (Figure 7.2). Vertical climb and descent were also found to have similar mean SS in both forest types. Orthograde locomotion (suspension and bipedalism) took place on significantly stiffer supports in mixed dry forest than observed in peat-swamp. Interestingly, whilst quadrupedalism took place on the stiffest supports in mixed dry forest, in peat-swamp forest, quadrupedalism took place on much more compliant supports, which were more similar in mean SS to bridging and sway in dry forest, indicating the more frequent use of pronograde scrambling than was observed in dry forest. For the interaction between habitat and age-sex class, it is clear that orangutans in dry forest

Figure 7.1 – Tukey's homogenous subsets (dashed boxes) and 95% confidence intervals for mean stiffness score (cm)

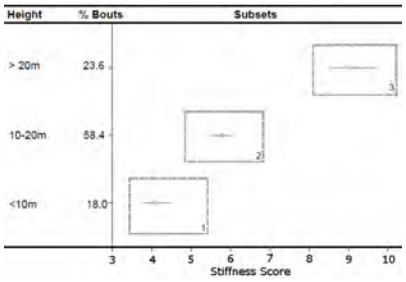
a) Locomotion[a]



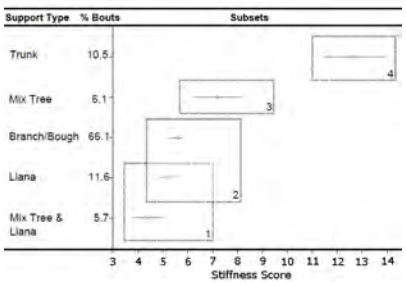
b) Age-sex class



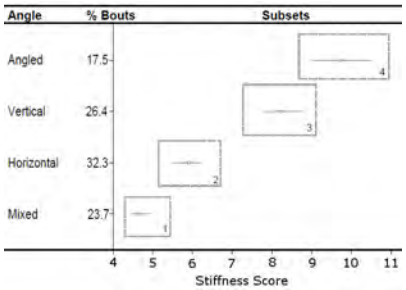
c) Height in the Canopy



d) Support Type

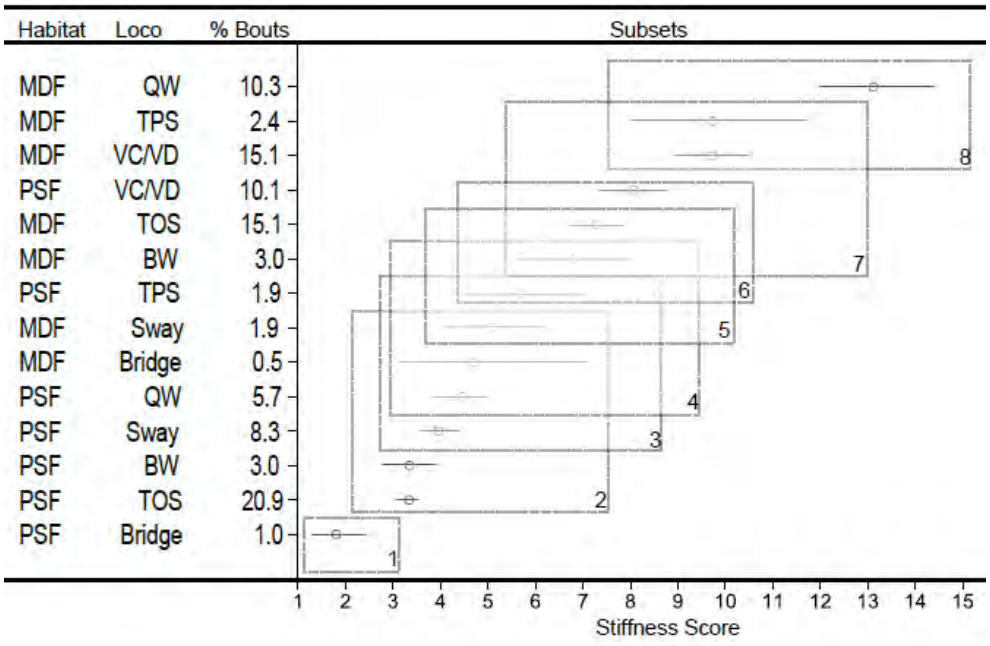


e) Support Angle



[a] Locomotion: VC/VD, vertical climb/descent; QW, quadrupedal walk; TPS, torso-pronograde suspension; BW, bipedal walk; TOS, torso-orthograde suspension; Sway, includes modes tree-sway and ride; Bridge, pronograde bridging.

Figure 7.2 – Tukey's homogenous subsets and 95% confidence intervals for the interaction: Habitat[a] * Locomotion[b]

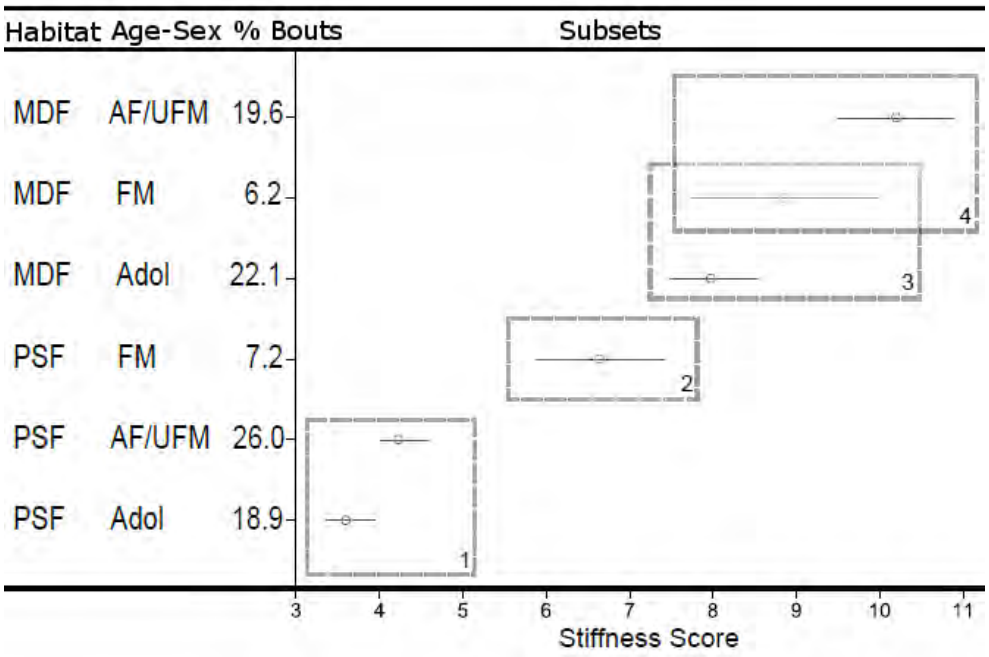


[a] Habitat: MDF, mixed dry forest (Ketambe); PSF, peat-swamp forest (Suaq Balimbing)
[b] Locomotion: VC/VD, vertical climb/descent; QW, quadrupedal walk; TPS, torso-pronograde suspension; BW, bipedal walk; TOS, torso-orthograde suspension; Sway, includes modes tree-sway and ride; Bridge, pronograde bridging.

use significantly stiffer supports than in peat-swamp (Figure 7.3). In fact, flanged males inhabiting peat-swamp use significantly more compliant supports than the much smaller non-sexually active females inhabiting dry forest. In peat-swamp forest the increase in mean SS follows an increase in body mass, whereas in mixed dry forest, it is sexually active females and unflanged males which used the stiffest supports, although these were not significantly higher than for flanged males (Figure 7.3, subset 4).

The interaction between angle and habitat highlights some interesting differences between the two forest types (Figure 7.4). For peat-swamp

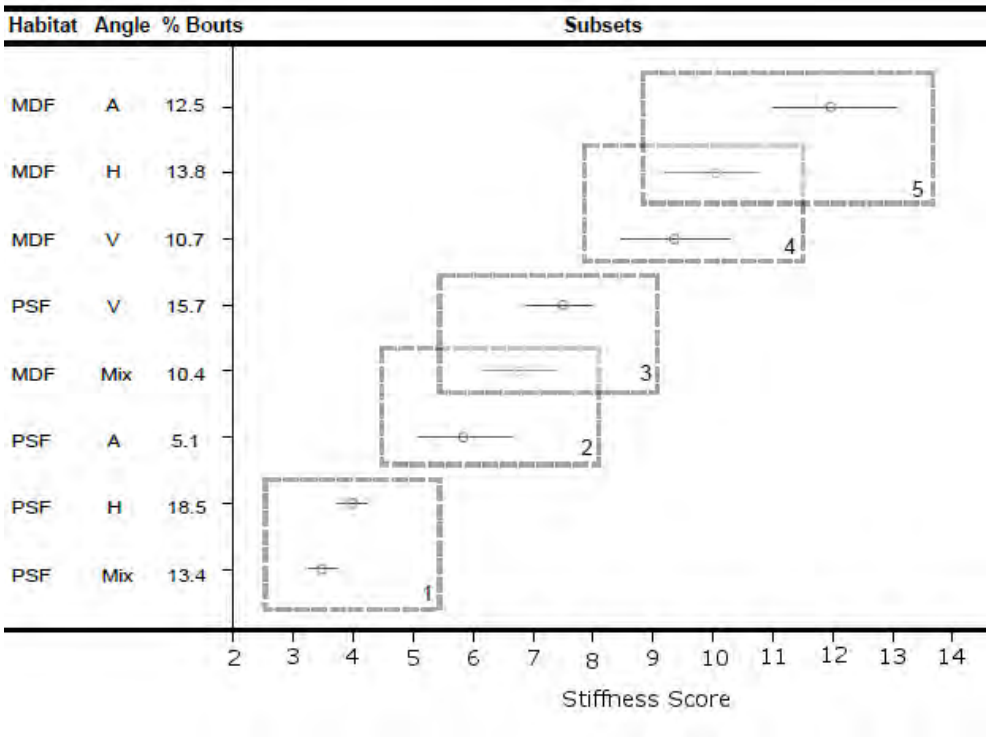
Figure 7.3 – Tukey's homogenous subsets and 95% confidence intervals for the interaction: Habitat[a] * Age-Sex[b]



[a] Habitat: MDF, mixed dry forest (Ketambe); PSF, peat-swamp forest (Suaq Balimbing).
[b] Age-Sex: AF/UFM, adult female/unflanged male; FM, flanged male; Adol, adolescents

forest, vertical supports had the highest mean SS, reflecting the higher use of tree trunks, whereas in mixed dry forest it is angled supports followed by horizontal supports, reflecting the higher frequency of the use of stiffer branches and boughs. In both forest types, supports of mixed angles had the lowest mean SS, although this was significantly lower in peat-swamp than in dry forest. The interaction between habitat and support type reveals that in both forest types the stiffest supports used for locomotion are tree trunks (Figure 7.5). The supports with the lowest mean stiffness score in peat-swamp forest were branches and boughs, whereas these were the second stiffest support type in mixed dry forest. Lianas were the most compliant support used for locomotion in mixed dry forest, whereas branches and/or boughs and the combined use of lianas and tree supports

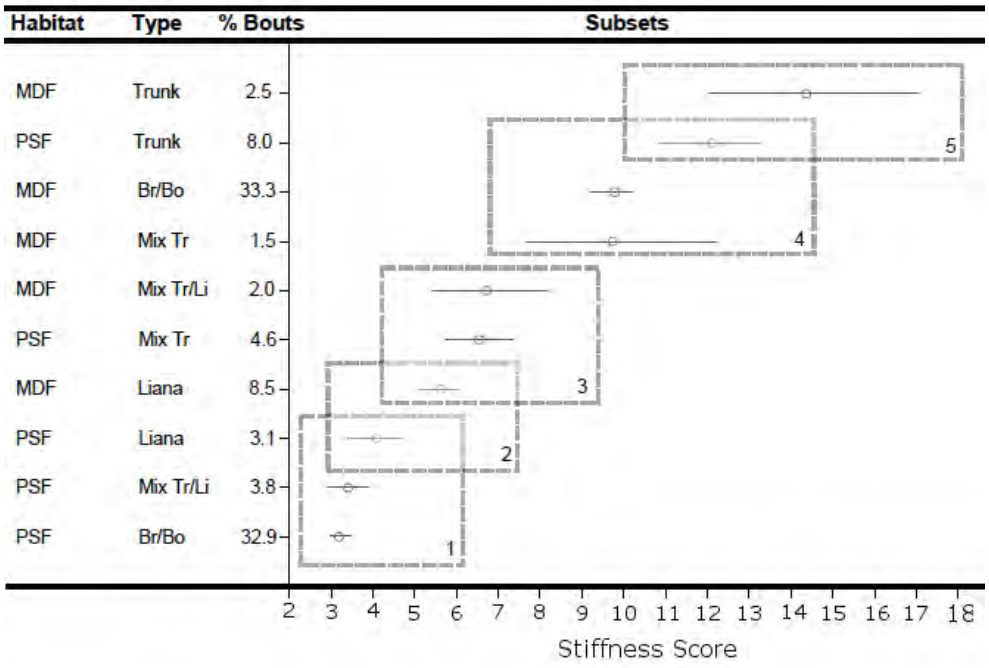
Figure 7.4 – Tukey's homogenous subsets and 95% confidence intervals for the interaction: Habitat[a] * Angle[b]



[a] Habitat: MDF, mixed dry forest (Ketambe); PSF, peat-swamp forest (Suaq Balimbing).
[b] Angle: A, angled; H, horizontal; V, vertical; Mix, any combination of angled and/or horizontal and/or vertical

allowed locomotion on the most compliant supports in peat-swamp. However, the mean SS for lianas was similar in both forest types (Figure 7.5, subset 2). Whilst the same trend between height in the canopy and habitat was the same between forest types the overall mean stiffness score for all heights was significantly greater in mixed dry forest than in peat-swamp (Figure 7.6).

Figure 7.5 – Tukey's homogenous subsets and 95% confidence intervals for the interaction: Habitat[a] * Support Type[b]

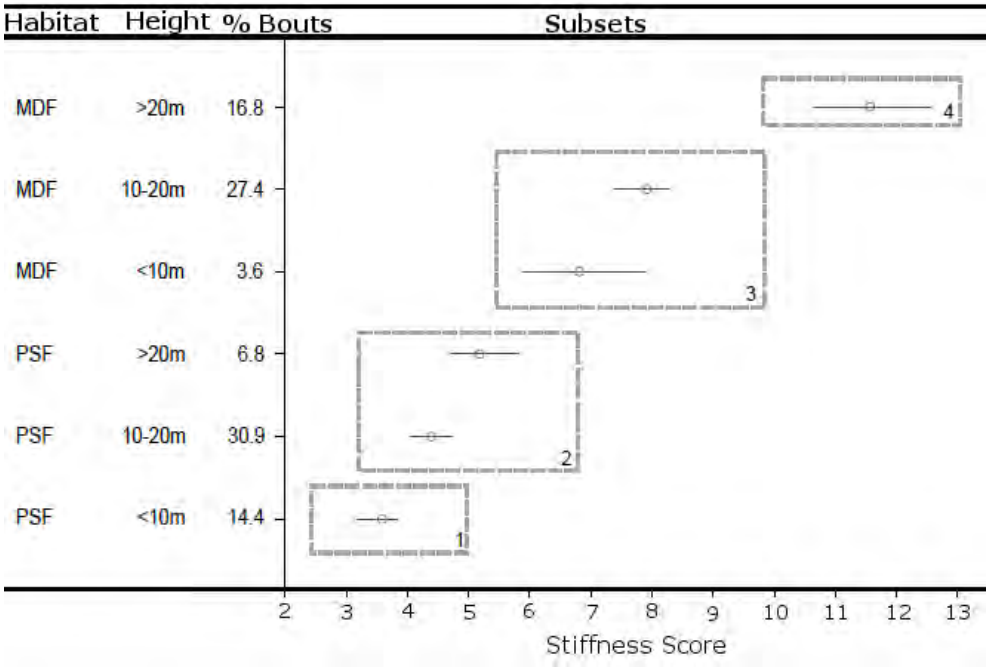


[a] Habitat: MDF, mixed dry forest (Ketambe); PSF, peat-swamp forest (Suaq Balimbing).
[b] Support Type: Br/Bo, branch/bough, Mix Tr, trunk and or branch/bough; Mix Tr/Li, liana and or trunk and/or branch/bough

7.4 Discussion

Accessing the terminal branch niche for both food as well as when traversing the canopy via the narrowest gaps between tree crowns presents substantial energetic demands, as well as safety risks for large-bodied primates, particularly orangutans. Thorpe et al. (2009) suggested that orangutans will use locomotor/support combinations close to the minimum threshold for compliant supports, to decrease the energetic cost of travel through reduced path length. Our prediction (Hypothesis 1) that orangutans in a more stunted peat-swamp forest with a more open canopy, and therefore less overlap of tree crowns, coupled with fewer large branches

Figure 7.6 – Tukey's homogenous subsets and 95% confidence intervals for the interaction: Habitat[a] * Height



[a] Habitat: MDF, mixed dry forest (Ketambe); PSF, peat-swamp forest (Suaq Balimbing).

will mean that orangutans inhabiting peat-swamp forest will be forest to travel closer to these minimum thresholds than orangutans in dry lowland forest was generally upheld. Orangutans in peat-swamp forest overall used significantly more flexible supports than orangutans in dry lowland forest, although some trends between the two forest types were apparent. We would expect tree-sway, a behaviour which relies on the use of compliant supports, to utilize supports of a similar flexibility, regardless of forest type, and this was found to be the case here. In addition, vertical climb/descent, a behaviour which is energetically costly because climbing directly opposes gravity, was exhibited on similarly stiff supports across the two forest types. Orangutans used relatively small supports for climbing probably to avoid the increased demand associated with employing extended-elbow "bear

climb", which is required to ascend supports with a large diameter (Isler and Thorpe, 2003), and the mean stiffness of supports used in both forest types may signify an optimum support size for energetic efficiency during climbing. For negotiating the most compliant supports, pronograde bridging was used in both forest types, further emphasising the special role of this behaviour for gap crossing as it enables orangutans to deal with the most flexible of branches, through a combination of unpatterned gait, with limbs in either compression or suspension, or both (Thorpe et al., 2009). Orthograde locomotion, including both orthograde suspension and bipedalism, are both associated with accessing the terminal branch niche (Thorpe et al., 2007b, 2009). Suspensory locomotion and particularly, orthograde suspension, are considered key adaptations for dealing with small, compliant supports as they theoretically reduce the risk of falling since body mass is already positioned below the support (Grand, 1972; Cartmill, 1985a; Hunt, 1992, Hunt et al., 1996; Pilbeam, 1996; Larson, 1998; Crompton et al., 2008). Additionally, hand assisted bipedalism has been shown to allow orangutans access to supports which are otherwise too compliant to be negotiated (Thorpe et al., 2007b). Whilst the mean compliance score for both orthograde suspensory locomotion and bipedalism was lower in peat-swamp than in dry lowland forest, they were not significantly different across the two forest types. In support of Hypothesis 2, we found a similar trend with regard to height in the canopy across the two forest types. Orangutans in peat-swamp forest also used stiffer supports with increasing height, although these supports were significantly stiffer in dry lowland forest. This is not surprising since dry lowland forest has a much higher abundance of larger supports than peat-swamp forest, thus while orangutans in peat-swamp select for the

largest supports that are available (in Chapter 4 we found that orangutans used larger supports more frequently than their availability), these supports are still likely to be smaller than in dry lowland forest. That orangutans use stiffer supports at greater heights highlights the importance of increased safety when moving high in the canopy, where the risk from falls is much more severe than at lower levels.

Our prediction that there would be little difference in the mean compliance score across the age-sex classes was not upheld in this study (Hypothesis 3). The relationship between support compliance and body size differed between the two forest types; in Ketambe sexually active females selected the stiffest supports, which was attributed to the tendency of sexually active females towards more conservative locomotor behaviour due to experience of raising offspring (Thorpe et al., 2009). In contrast, in Suaq Balimbing, sexually active females and unflanged males used similarly compliant supports to those used by non-sexually active females, whereas flanged males used the stiffest supports. These results support our prediction that there would be little variation between age-sex classes given the use of arboreal pathways by all individuals in the population, since only flanged males used significantly stiffer supports than the other age-sex classes. However, our prediction that adult females might use the stiffest supports for increased safety was not upheld. That orangutans in peat-swamp forests use increasingly stiff supports with increased body mass suggests that when dealing with smaller, more compliant supports body mass plays a more important role and supports which the smaller bodied age-sex classes are able to negotiate are too small for the heavier flanged males.

We predicted that orangutans in peat-swamp forest would have a different relationship with the type of supports than orangutans in dry lowland forest (Hypothesis 4), and this was found to be the case. Whilst orangutans at both sites used trunks and lianas of similar stiffness, the biggest difference observed between the forest types with regard to support type was that of the stiffness of branches and boughs. In peat-swamp forest locomotion on branches and boughs was on the smallest, most compliant supports, in stark contrast to the behaviour of orangutans in dry lowland forest where the branches and boughs used for locomotion were significantly stiffer. In Chapter 4 we found that Ketambe had a significantly higher abundance of larger branches and boughs than Suaq Balimbing, coupled with a more closed canopy, and therefore crowns with a greater degree of overlap, thus theoretically allowing orangutans to transfer between tree crowns using stiffer, more stable supports, thereby reducing the necessity for travel in the peripheral branches. The results of this study suggest that orangutans in Sumatran peat-swamp forest more frequently need to cross the crowns of trees via the thin peripheral branches forcing them to travel closer to the minimum

'threshold of locomotor/support combinations than orangutans inhabiting dry lowland forest.

Our prediction (Hypothesis 5) that orangutans in peat-swamp forest would have a different relationship with support compliance and support angle than in dry lowland forest was upheld. The stiffest supports used in peat-swamp were vertical supports highlighting the increased frequency of trunk use in peat-swamp forest. In contrast, the stiffest supports used in dry

lowland forest were those which were angled and angled supports were used at a much lower frequency in peat-swamp than in dry lowland forest. However, the most compliant supports used in both forest types were those of mixed angle, indicating that orangutans use the most compliant supports by distributing their weight over supports of different orientation, which confers benefits in controlling support compliance as the different orientation of the supports used may help counter the effect of compliance in each individual support (Thorpe et al., 2009). These results suggest that the complexity of support orientation may be as challenging as support compliance for arboreal locomotion. In a study of energy exchange during brachiation in Siamang (*Symphalangus syndactylus*), the orientation of handholds was found to have equal effect as their spatial complexity (i.e. arrangement at different heights) on energy recovery (Michilsens et al., 2011).

Together these results suggest that orangutans in both dry lowland forest and peat-swamp forest deal with the most compliant supports through distributing their weight over multiple supports with a combination of both orthograde and pronograde postures, both in compression and suspension (Thorpe et al., 2009). However, orangutans in peat-swamp use more compliant supports than was observed in dry lowland forest. This suggests that orangutans in dry lowland forest are not travelling close to the minimum thresholds of support compliance but, as a result of their environment, prefer to use single supports with a mean compliance of not much less than 6 cm and multiple supports with a mean compliance of 3.5 cm per support. In contrast, in peat-swamp forest, orangutans are forced to travel closer to the minimum threshold as hypothesised by Thorpe et al.

(2009) in order to reduce vertical displacement and thus path length, by negotiating the terminal branches in order to transfer across tree crowns in a forest with a more open canopy.

7.5 Conclusions

Orangutans in peat-swamp used more compliant supports than were observed in dry lowland forest. However, in both forest types, orangutans used pronograde bridging to negotiate the most compliant supports. As was observed in dry lowland forest, orangutans inhabiting peat-swamp also use stiffer supports when travelling at higher levels in the canopy, highlighting the increased importance of safety at greater heights. Sexually active females did not use the stiffest supports in peat-swamp, rather, the larger-bodied flanged males used the stiffest supports indicating that when dealing with smaller, more compliant supports, body mass plays a more important role in support selection. Orangutans in both peat-swamp and dry lowland forest used lianas and trunks of similar size, however, for branches and boughs, supports were much stiffer in dry lowland forest. The most compliant supports used in both forest types were those of mixed angle indicating that orangutans are able to deal with support compliance by distributing their weight over supports of different orientation, which may help counter the effect of compliance in each individual support.

CHAPTER 8

General Discussion

8.1 Introduction

THE primary objective of this thesis was to expand understanding of orangutan locomotion and how it relates to forest structure and species differences between Borneo and Sumatra. At the outset, we did this by undertaking an in-depth study of the locomotor behaviour of wild orangutans in two peat-swamp forests, one in Borneo and one in Sumatra, in order to understand how locomotor behaviour in peat-swamp forest compares to that observed in dry lowland forest in Sumatra, where orangutan positional behaviour has been well-studied (e.g. Thorpe and Crompton, 2005; 2006; 2009; Thorpe et al., 2007a, b, 2009; Myatt and Thorpe, 2011). Secondly, we undertook a quantitative assessment of forest structure and support availability in three orangutan study-sites for which we had detailed information on positional behaviour. This enabled a comparison of structural features of each forest and advance our understanding of how orangutans interact with such a complex environment. Finally, we used a

non-invasive technique to obtain measurements of limb lengths in both orangutan species, as well as from an orangutan rehabilitation centre in Borneo, to compare the limb lengths of the two species. As a consequence we have contributed to current understanding of the dynamic between morphology, behaviour and habitat in the largest arboreal primate.

8.2 Summary of Main Results

Locomotion in Disturbed Peat-Swamp Forest

In chapters 2 and 3, we analysed the locomotor behaviour of a population of wild orangutans inhabiting disturbed peat-swamp forest, a habitat in which orangutan locomotion had never previously been studied in detail. Some of the major findings of this study included the fact that the more homogenous forest structure of disturbed peat-swamp forest appears to limit orangutans to higher frequencies of fewer behaviours and there were much higher levels of tree-sway in disturbed forest; the high density of small tree trunks may fulfil a functional role to that of lianas; the most important distinction for locomotion was between suspension and compression, although the distinction between orthograde and pronograde locomotion was also important; finally, our research added support to the suggestion that adult females are more conservative in their locomotor behaviour than other age-sex classes (Thorpe and Crompton, 2005; Thorpe et al., 2009).

We found that overall orangutans exhibit the same breadth of locomotor behaviour, with orthograde suspension dominating orangutan locomotor behaviour, regardless of habitat type. This is not surprising since the non-human apes as a group are characterised by orthograde behaviours

(Thorpe and Crompton, 2006; Crompton et al., 2008), and suspensory locomotion confers significant benefits for increased safaty and stablity in an arboreal environment (Carmill, 1985; Cartmill and Milton, 1985). That locomotion in disturbed peat-swamp forest was best understood in terms of suspension and compression contrasts with what was found in dry lowland forest, where distinction was made between a larger number of categories (Thorpe and Crompton, 2005). Furthermore, we found that orangutans in disturbed peat-swamp exhibited higher frequencies of fewer behaviours, indicating that orangutan locomoton may be more restricted by the homogeneity of disturbed forest. Suspensory locomotion was observed at a higher frequency in disturbed peat-swamp compared to dry lowland forest, which suggests that the lack of large supports in disturbed forest (chapter 4) forces orangutans to employ more suspensory locomotion, since as support diameter decreases it becomes more difficult to maintain balance in compression, whereas suspension enhances stability, as the animal has, in effect, already fallen off (Cartmill, 1985).

The high incidence of tree-sway in disturbed forest is interesting for two main reasons; firstly, it has been identified as the most energetically efficient method of gap crossing (Thorpe et al., 2007a) and secondly, orangutans in disturbed peat-swamp forest have been found to experience levels of negative energy balance (Harrison et al., 2010). Therefore this strategy may help to reduce energy expenditure during travel, thereby mitigating some of the impacts of forest disturbance on orangutan populations.

This study (chapter 3) also found that small tree trunks played a key role in the locomotor behaviour of orangutans in disturbed peat-swamp. Tree

trunks were an important support for both orthograde locomotion (particularly orthograde clamber), vertical climb and descent as well as tree-sway. Trunks were the dominant support type used below 10m. We suggested in chapter 3 that small compliant tree trunks in disturbed forest fulfil a functional role played by lianas in more pristine habitat. This supports Cant's (1992) suggestion that in forest that has low liana density, orangutans may be more likely to cross gaps by tree-swaying using vertical trunks. In addition, where lianas had been identified as an important support for accessing large feeding trees in dry lowland forest (Cant, 1992; Thorpe and Crompton, 2005), in disturbed peat-swamp forest the trees themselves were sufficiently small enough to be climbed with a flexed elbow. This negated the necessity for liana use, even when present, to prevent climbing using the more demanding "bear climb". Thus, it is not necessarily the actual density of lianas that limits their use, but rather that a higher density of smaller trees in the disturbed peat-swamp forest not only facilitates tree-sway, but also reduces the requirement for lianas as a support for climbing as well as limits the opportunites for lianas to provide arboreal pathways for orangutans.

Both flanged males and adult females used single small supports at a low frequency (chapter 3), and adult females selected larger trees for locomotion than other age-sex classes (chapter 4). This indicates that flanged males are too heavy to use the smallest supports unless their body mass is distributed over multiple supports while adult females, as a result of experience with raising offspring, are more cautious in their locomotor behaviour as was found in dry lowland forest in Sumatra (Thorpe and Crompton, 2005; Thorpe et al., 2009).

Habitat Structure and Species Variation

The results of chapters 2 and 3, led us to consider that habitat was responsible for much of the variation in orangutan locomotor behaviour. In chapter 4 we quantified forest structure and support availaibility so we could better understand the effect of habitat on orangutan locomotion. We found that there was a large degree of difference between the three sites included in this study in terms of tree and liana density, but that the two peat-swamp forest sites were generally more similar to each other than either were to the dry lowland habitat. Orangutans in all three sites did not substantially differ in terms of their preferred supports. However, orangutans in Sumatra demonstrated a strong preference for liana use, not observed in the disturbed peat-swamp forest in Borneo (chapter 4). This added further support to our suggestion that the extremely high density of small tree trunks fulfils a functional role provided by lianas in other forests (chapter 3). Futhermore, the way in which support types were conflated (i.e. as a proxy for support orientation) to produce the best-fitting model in chapter 6, indicates that the orientation of supports is the most important distinction in terms of orangutan locomotor behaviour, adding further support to this suggestion. Dry lowland forest had the most heterogeneous structure, with a much wider range of supports of varying size and type and this appears to have facilitated their more varied locomotor repertoire.

Whilst we attributed many of the differences in locomotor behaviour to habitat variation, we were interested to establish if there were any differences between the Sumatran species (*P. abelii*) and the Bornean sub-species (*P. p. wurmbii*) in terms of their limb lengths (chapter 5). Whilst the sample size obtained in this study is rather small, as is often the case

with studies of apes, our results indicate that there is little difference in limb length between the two species, despite there being differences in their cranio-dental morphology (Taylor, 2006, 2009; Taylor and van Schaik, 2007). This suggests selection for optimal limb lengths, as they are likely to confer benefits for an arboreal lifestyle, particularly reach and gap crossing, which may outweigh the additional costs associated with maintaining large body size. This is particularly important for the Bornean sub-species which is known experience periods of energetic stress, as a result of the lower quality forest (chapter 1). However, there are no known weights for wild Sumatran orangutans and they may have a larger body mass than their Bornean counterparts. Furthermore, limb lengths are only one aspect of the postcrania likely to effect locomotor behaviour and there may be more subtle differences in the morphology between the two species.

The data on rehabilitant orangutans from Nyaro Menteng yielded some interesting results (chapter 5). We found that in terms of limb length there was little difference between the two male morphs, with unflanged males having similar limb lengths to flanged males. Therefore, it would appear that the development of secondary sexual characteristics is associated with weight gain rather than skeletal growth. We also found that males and females, when scaled for body mass were similar indicating that males and females are isometrically similar, with males essentially being larger versions of females.

The Effect of Habitat and Species Variation on Orangutan Locomotion

Both species diversity and habitat structure have the potential to cause variation in locomotor behaviour among arboreal primates. In chapter 5, we combined data from three orangutan study sites, in order to compare both orangutan species in different forest types thereby increasing our understanding of ecological differences, through rigorous statistical testing. Therefore, this was the first study to employ a multivariate statistical approach to investigate whether the greatest differences in observed orangutan locomotor behaviour are at the species or habitat level, by examining the association between orangutan locomotion and support characteristics (diameter, type and number of supports used).

Our results imply that differences in support use during locomotor behaviour are a consequence of forest structure, since habitat produced a stronger model than either species or study site (chapter 5), indicating that the way in which orangutans solve problems associated with arboreal travel reflects the structure of the forest. In the analysis, locomotion was best described very simply, in only three categories, which are based on the orientation of the torso. We might have expected the difference between suspensory and compressive locomotion to be more important when comparing habitat type, with orangutans in more stunted peat-swamp forest to exhibit more suspensory behaviour, using multiple small supports (chapter 2 and 3), whereas orangutans in dry lowland forest, where there is a higher prevalence of stiffer supports, might be expected to exhibit higher frequencies of the more energetically efficient compressive locomotion (chapter 4), but this was certainly not the case. However, these combinations

performed reasonably well in both Thorpe and Crompton's (2005) study in dry lowland forest in Sumatra, as well as in disturbed peat-swamp forest in Borneo (chapter 2).

What is perhaps more interesting is that orangutan locomotion had a stronger association with support characteristics than any influence of habitat. This in all likelihood indicates that the commonalities of orangutan locomotor behaviour are more important than any differences imposed by forest structure. This is an interesting result as it suggests that orangutan locomotion has evolved to be so plastic that despite even fundamental structural habitat differences, locomotor behaviour doesn't really differ.

However, there are some differences between forest types in how orangutans oscillate supports, particularly for multiple branches/boughs, which were used at much higher frequency in dry lowland forest compared to peat-swamps. Orangutans in both peat-swamp sites frequently swayed trees about the trunk using body mass alone, whereas in dry lowland forest orangutans were required to distribute their body weight over multiple supports in order to gain the required magnitude to bridge a gap.

Orangutans are predominantly orthograde in posture and orthograde locomotor behaviour tended to be associated with multiple vertical supports (i.e. trunks or lianas), whereas pronograde behaviour was more associated with horizontal or angled supports (i.e. branches or boughs). Oscillation, which involves both orthograde and pronograde postures, tended to be exhibited on single vertical supports or a combination of vertical and horizontal/angled supports. Thus, the orientation of the trunk

is more important, than whether or not the orangutan is on top of, or in suspension underneath a support, for solving problems associated with habitat. This is interesting given theoretical predictions that suggest suspensory postures should increase with increased body mass (Cartmill and Milton, 1977) and that orthograde suspension is considered to be a primary mechanism to enable large-bodied apes to solve problems in negotiating small peripheral branches (Grand, 1972; Cartmill, 1985b; Cant, 1992). However, recent studies of orangutan positional behaviour have found that hand-assisted bipedalism which is an orthograde compressive behaviour (Thorpe et al., 2007b); pronograde bridging which is a mixture of compressive and suspensory behaviour (Thorpe et al., 2009) and pronograde suspensory posture during feeding in the terminal branch niche (Myatt and Thorpe, 2011) are used to solve problems associated with small, compliant supports, rather than orthograde suspension. This highlights the plasticity of orangutan locomotor behaviour when negotiating small, compliant supports. The results of this study further our understanding of how orangutans interact with their environment and how adaptable they are to differences in forest structure and forest disturbance.

Whilst orthograde behaviour dominates orangutan locomotion, it is pronograde behaviour, specifically bridging and suspension, both of which are rare or non-existent in other great apes, that enables orangutans to negotiate the smallest most compliant supports, thus highlighting specialisations for arboreal locomotion.

Orangutan locomotion had a stronger association with support characteristics than any influence of habitat. This indicates that the

commonalities of orangutan locomotor behaviour are more important than any differences imposed by forest structure and the associated distribution and abundance of supports of differing sizes and types.

Since habitat type had more of an influence on orangutan locomotion we wanted to further investigate the relationship between habitat and support use during locomotion. Thus, in chapter 7 we compared the compliance of supports (as estimated from stiffness score) used by Sumatran orangutans (*Pongo abelii*) in two distinct forest types: dry lowland forest and peat-swamp forest. Orangutans in peat-swamp forest generally used more compliant supports than in dry lowland forest although some patterns between the two forest types were apparant. Pronograde bridge took place on the most compliant supports in both forest types although these were more compliant in peat-swamp forest (chapter 7). This further demonstrates that orangutans deal with the most compliant supports through distributing their weight over multiple supports with a combination of both orthograde and pronograde postures, both in compression and suspension (Thorpe et al., 2009). Orangutans in peat swamp also used stiffer supports when travelling higher in the canopy, to presumably increase safety as injuries from falls are likely to be much more severe with increased height.

The most compliant supports used in both forest types were those of mixed angle indicating that orangutans are able to deal with support compliance by distributing their weight over supports of different orientation, which may help counter the effect of compliance in each individual support. Apart from using more compliant supports overall, the main difference observed between the two forest types was that flanged males used the stiffest

supports, not adult females, indicating that when dealing with smaller, more compliant supports, body mass plays a more important role in support selection. This was also found in peat-swamp forest in Borneo (Phillips, 2011). Adult females used similarly compliant supports to adolescents, which are of a similar size and weight, and unflanged males which are heavier (chapter 5). This would indicate that the locomotor behaviour of adult females is no more conservative than that of other age-sex categories in this forest, and that the selection of travel routes is based on crown connectivity to reduce path length, as a consequence of the more open canopy (chapter 4).

8.3 Implications for Orangutan and Hominoid Evolution

Based on the analysis of genetic data, the genetic diversity of orangutans is though to be higher in Sumatra than Borneo (Steiper, 2006) and extensive gene flow between Bornean and Sumatran populations probably did not take place during the Pleistocene. Relatively recent synthesis of genetic, palaeoclimatic, palaeontological and zoo-archaeological data supports a model whereby orangutans entered Sundaland around 2.7 Ma, with population fragmentation at 1.8 Ma (Harrison et al., 2006). Even though the Sunda shelf was cyclically exposed during this period, it is suggested that as the habitat was not well suited to arboreal primates (i.e. grasslands and drier, more seasonal woodland) coupled with large river systems, the gene flow between Borneo and Sumatra was restricted, whilst during the same period intermittent land bridges between Sumatra and the mainland maintained gene flow between these two populations (Harrison et al., 2006).

Furthermore, the eruption of the Toba volcano (75,000 ya) would have likely decimated the vast majority of the Sumatran orangutan population (Muir et al., 2000), which was most likely replenished by immigrations from Peninsular Malaysia. Thus, the more recent mingling with the ancestral mainland population would make the Sumatran orangutan the best model for the ancestral orangutan.

The results of this study suggest that variation in habitat structure have more of an influence orangutan locomotor behaviour than any inter-specific differences. Consequently, we are more likely to gain a better understanding of the pressures that shaped orangutan evolution by examining present day orangutans in habitats more similar to those which were inhabited by ancestral orangutans. It has been suggested that greater inference can be drawn from observations of Bornean orangutans in masting habitats such as Gunung Palung and Kutai as these considered to have the same levels of forest productivity as the ancestral orangutan inhabited (Harrison 2009b). Sumatran forests are more productive than Bornean forests, regardless of forest type as a result of the former's younger more fertile volcanic soils compared to the latter's older sedimentary rocks (Marshall et al. 2009) and probably mainland Asia, where rocks in many regions date back to the Palaeozoic era (540-248 Ma, Whitten et al., 2000). Furthermore, peat swamp forest is unevenly distributed throughout South-East Asia and the majority is found in Indonesia (82% of the total area of peat swamp forest in South-East Asia, Reiley et al., 1996) and it is therefore unlikely that the common orangutan ancestor inhabited this type of environment. Dipterocarp pollen has been found in Pleistocene marine cores from the Banda Sea on the Sunda Shelf (van der Kaars et al., 2000; Hope et al., 2004).

Dipterocarps tend to dominate in most contemporary South-East Asian forests in which they occur (Ashton, 1988). Whilst the extent of these forests is likely to have expanded and contracted in response to climate change it remains likely that dipterocarp forests persisted throughout Peninsula Malaysia and were the main orangutan habitat during this period (Jablonski, 1997, 1998; Jablonski et al., 2000). Therefore it is likely that the orangutans ancestor underwent the majority of its evolution on mainland South-East Asia, and most likely in dipterocarp forests with a similar forest productivity to Bornean masting forests. Thus it has been suggested that orangutans in Bornean masting forests are likely to provide the best model of the ancestral orangutan (Harrison, 2009a).

Whilst Bornean forests might be similar in terms of productivity (as defined here as orangutan fruit availability), which would in turn influence foraging behaviour. It is feasible that lowland dipterocarp forest has a similar structure to lowland dipterocarp forest in Borneo (we found in this study that although Sumatran peat-swamp is more productive than Bornean peat-swamp they were not particularly dissimilar in terms of their structure and support availability), although detailed comparisons of forest structure between dipterocarp forest on Borneo and Sumatra are needed to confirm this suggestion. If it is the case that the structure of lowland dipterocarp forest is similar across both islands, we suggest that the best model of the ancestral orangutan, in terms of positional behaviour could be Sumatran orangutans (as a result of the closer genetic history) inhabiting masting dipterocarp forests (the ancestral habitat). This would lead us to consider that the common ancestor of extant Sumatran and Bornean orangutans is likely to have had a locomotor behavioural profile more similar to

orangutans in Ketambe, Sumatra than those inhabiting peat swamp forest in either Sumatra or Borneo, given the presumably more similar forest structure to the ancestral habitat. Thus, the orangutan ancestor is likely to have exhibited higher frequencies of pronogrady, both in compression and suspension, as well as higher frequencies of bipedalism and climbing, than present day orangtuans inhabiting peat swamp forests.

The results of this study indicate that, whilst habitat has an important influence on orangutan locomotor behaviour, the similarities between orangutans, both between species and habitat types, in their overall behavioural repertoire and their approach to locomotion (i.e. the type and size of supports selected for specific behaviours) indicates that orangutan locomotion is extremely plastic. In forests which are structurally different, orangutan locomotion remains essentially the same, and merely the frequency of observed behaviours alters. In addition, common behaviours remain common and although orangutans have an extremely diverse repertoire (Thorpe and Crompton 2005, 2006, this study), orthograde suspensory locomotion dominates. Although orangutans do employ compressive quadrupedalism (as do Pan spp) it is thought that pronograde suspensory locomotion is unique among orangutans (Thorpe and Crompton, 2006). The use of pronograde suspension by orangutans both as a locomotor behaviour and as an important posture for feeding in the small, peripheral branches (Myatt and Thorpe, 2011) and not by other great apes (Hunt, 1991, 1992a,b; Doran, 1993aa,b; Fleagle, 1999) indicates that this behaviour evolved in orangutans after their split from the common great ape ancestor, presumably as a result of their predominantly arboreal lifestyle (Thorpe et al., 2009; Myatt and Thorpe, 2011). Whilst last common great ape

is likely to have been arboreal [see review in Crompton et al. (2008)], it has been proposed that orangutans evolved pronograde suspensory locomotion in parallel with the terrestrial quadrupedalism employed by African apes (Crompton et al., 2008; Elton, 2008; Thorpe et al., 2009).

The combination of both orthograde suspensory behaviour and quadrupedal palmigrady adaptations in Hispanopithecus laietanus suggests a unique positional repertoire and indicates that locomotor evolution in the Hominoidea evolved in a mosaic fashion (Almécija et al., 2007; Alba et al., 2012). It is now widely accepted that across hominoid lineages, it is an upright (orthograde) truncal posture which is the common inheritance from the last common great ape ancestor. Whilst orangutans are likely to have become more specialised for their arboreal lifestyle since their split from the last common ancestor, since they are the only living great ape to have retained a fully arboreal lifestyle, they provide an opportunity to asses locomotor behaviour by a large-bodied ape in an environment similar to that inhabited by the last common ancestor, which is not possible in African apes given their conflicting adaptations to their terrestrial habitat (Myatt and Thorpe, 2011). The results of this study support the suggestion that whilst orthograde behaviour in general characterises the non-human apes, it would appear that pronograde behaviour (specifically bridging) enables orangutans, the arboreal specialist, to negotiate the smallest peripheral branches (Thorpe et al., 2009) and that the orientation of the torso is what enables orangutans to find solutions to negotiating such a complex arboreal environment.

8.4 Ideas and Recommendations for Future Research

Comprehensive studies of orangutan locomotion have thus far focussed on orangutans in one study site (Ketambe) and more recently peat-swamp forests (this study; Phillips, 2011). Therefore much remains to be discovered about their behaviour. The only study on the Bornean sub-species (*Pongo pygmaeus morio*) was conducted on only two adult females. It would be both interesting and important to obtain more detailed information on this sub-species because they inhabit the least productive habitat, have the lowest energy intake during extended lean periods, higher levels of folivory, the shortest inter-birth intervals, the most robust mandible and a significantly smaller cranial capacity compared to most other orangutans groups (Taylor and van Schaik, 2007). It would also be interesting to obtain more detailed data on the sub-species (*P. p. wurmbii*) in different forest types to increase our understanding of the extent of the impact of habitat variation on orangutan locomotor behaviour.

Gunung Palung would be an ideal site to study orangutan locomotion in the future as although it is in the main a truly masting dipterocarp forest and as such is likely to be similar to the ancestral habitat. However, it is also a mosaic of forest types containing seven habitats in total, including peat-swamp forest, alluvial bench, freshwater swamp, lowland granite, lowland sandstone, upland granite and montane forest (Marshall, 2010). Thus Gunung Palung would be an interesting site to investigate locomotor behaviour in habitat similar in productivity to that inhabited by the last common orangutan ancestor, and also locomotor plasticity between forest types within a population. Furthermore, as it is a truly masting forest, it woudl also be an ideal site for a longitudinal study to see if and how

locomotor behaviour alters during periods of high and low food availability.

There is currently little data on *P. p. pygmaeus* for much of their behavioural ecology and thus less is known about this sub-species than the other two Bornean sub-species. If any opportunities arise in which to study this lesser known species it would be important in increasing our understanding of the positional behaviour across the orangutan taxa.

The collection of energetic data in the wild is difficult and, as a result, kinematic data, oxygen consumption, bone strain or muscle activity, are studied in a laboratory. Video analysis is becoming much improved and can be used for the examination of gait choice footfall sequence and limb timing, contact times, limb protraction and retraction, elbow yield (see review in Schmitt, 2011). However, for orangutans obtaining sufficient video recordings can be difficult, especially for relatively rare behaviours, such as pronograde bridging which has been identified as being used on the most compliant supports and also likely to produce different stresses on the musculoskeletal system (Thorpe et al., 2009). However, whilst obtaining videos of wild behaviour is difficult, I would recommend the field site Suaq Balimbing for any future study of this nature, as the orangutans are firstly generally more visible than at other sites (Manduell, personal observations) and secondly there are likely to be more opportunities for videoing gap crossing behaviour as a result of the more open canopy. Nevertheless, cross-speciality collaborations between biomechanics specialists together with field researchers whose studies address both positional behaviour and feeding ecology is an important next step as this would undoubtedly provide more insight into the energetic intake/expenditure of these animals.

D'Aout and Vereecke's (2011) recent volume highlights the necessity for linking field and laboratory research with regard to primate locomotion.

More morphological work is certainly needed on all orangutan taxa. The measurements obtained from Nyaro Menteng provided a good starting point and it would be useful if other rehabilitation centres could take baseline measurement data to increase the data set on orangutan postcranial morphology for all taxa, and also longitudinal data on the infants so we can gain a better understanding of their development. Cadavers are rare, and ordinarily come from captive environments, which as a result of the relative impoverishment of their environment could potentially modify the musculoskeletal system (Sarmiento, 1986). Perhaps more work from fatalities of wild individuals, or rehabilitants who have been living in semi-wild conditions, could be undertaken in the future through collaborations with rehabilitation centres.

Whilst this study does have strong implications for conservation, as the data bears directly on the habitat requirements of these charismatic but endangered animals. I would recommend that future studies of orangutan locomotion have more of a conservation focus, as given their critically endangered (Sumatra) and endangered (Borneo) status this must be the ultimate aim. Examining the locomotor behaviour of rehabilitated orangutans pre-release to assess whether they have the necessary skills to survive in a wild environment is paramount. However, post-release monitoring of rehabilitant orangutans is also important in furthering our understanding of behavioural responses to changes in their environment. Also, investigating ways in which fragmented forests could potentially be

linked (e.g. through the creation of artificial pathways) might increase the number of areas available which can support minimum population sizes.

APPENDIX A

Study Subjects: Sabangau and Suaq Balimbing

Table A.1 – Sabangau Study Subjects

Age-Sex Category	Name	No. Focal Days
Adult/Flanged Male	Beethoven	3
	Jupiter	9
	Leonardo	1
	Mozart	7
	Oberon	3
	Peterpan	7
	Wallace	1
	Salvador	1
Adult Female/Sexually Active Female	Cleo	2
	Indah	14
	Eosah	1
	Viola	3
	Willow	2
Subadult/Unflanged Male	Archimedes	1
	Romeo	7
	Ulysses	4
	Zeus	3
	Xylon	3
	Bengy	4
	Orson	4
Adolescent Female/Non-Sexually Active Female	Feb	19
	Indy	8

Table A.2 – Suaq Balimbing Study Subjects

Age-Sex Category	Name	No. Focal Days
Adult/Flanged Male	Eddy	4
	Otto	2
	Wilson	2
Adult Female/Sexually Active Female	Cissy	2
	Dodi	2
	Friska	3
	Lisa	5
Subadult/Unflanged Male	Gura	2
	Ulysses	5
	Xenix	4
Adolescent/Non-Sexually Active Female	Tina	6
	Ellie	4
	Shera	4

APPENDIX B

Frequencies of Locomotor Modes

Table B.1 – Frequencies of Locomotor Modes

Locomotor Mode, *submode*[a]	**Ketambe**[b]	**Suaq Balimbing**	**Sabangau**
Quadrupedal Walk			
Symmetrical gait walk	8.00	5.10	4.20
Irregular gait walk (scramble)	9.36	5.60	4.30
Tripedal Walk			
Tripedal walk	0.22	0.10	-
Bipedal Walk			
Extended bipedal walk	1.28	0.40	0.10
Flexed bipedal walk	0.36	0.10	0.05
Hand-assisted extended bipedal walk	2.88	2.80	1.40
Hand-assisted flexed bipedal walk	0.57	0.20	0.40
Bipedal scramble	0.14	0.10	-

Locomotor Mode, *submode*[a]	**Ketambe**[b]	**Suaq Balimbing**	**Sabangau**
Hand-assisted bipedal scramble	2.03	1.80	1.30
Vertical Climb			
Flexed-elbow vertical climb	6.19	9.0	6.40
Inverted flexed-elbow vertical climb	0.50	0.10	0.10
Ladder climb	0.18	1.40	1.50
Vertical scramble	7.72	2.0	0.80
Extended-elbow vertical climb	1.63	0.50	0.80
Bimanual pull-up	1.32	0.20	0.20
Vertical climb forelimbs only	0.25	0.10	-
Vertical Descent			
Rump-first vertical descent	2.27	3.00	3.30
Rump-first scramble descent	4.91	1.30	0.50
Rump-first forelimbs only descent	0.74	0.10	0.10
Rump-first cascade descent	0.18	0.90	0.50
Rump-first extended elbow descent	0.35	0.10	0.10
Fire pole slide	0.22	0.30	0.10
Head-first descent (scramble)	0.47	0.40	0.30
Head-first descent (cascade)	0.07	0.40	0.20
Pronograde slide	0.08	0.10	-
Sideways vertical descent	1.39	0.10	0.05
Cartwheel descent	0.21	0.20	0.10

Locomotor Mode, *submode*[a]	**Ketambe**[b]	**Suaq Balimbing**	**Sabangau**
Torso-Orthograde Suspensory Locomotion			
Brachiate	6.15	7.60	4.00
Forelimb swing	8.25	5.90	2.70
Flexed-elbow forelimb swing	0.18	0.30	0.20
Orthograde transfer	6.05	4.80	5.00
Orthograde clamber	14.37	21.30	35.90
Arrested drop	0.85	0.20	0.05
Torso-Pronograde Suspensory Locomotion			
Inverted quadrupedal walk	2.28	2.80	0.40
Inverted tripedal walk	0.11	-	0.05
Inverted quadrupedal run	0.04	-	-
Inverted pronograde scramble	1.28	0.60	0.70
Hindlimb Swing	0.14	0.10	0.10
Forelimb-Hindlimb Swing			
Cartwheel swing	0.18	0.10	0.05
Ipsilateral swing	0.07	1.90	1.00
Bridge			
Cautious pronograde bridge	2.53	1.40	1.60
Inverted pronograde bridge	0.11	0.10	0.10
Lunging bridge	0.14	0.40	0.20
Supinograde bridge	0.04	-	-
Descending bridge	0.04	-	0.05
Leap			
Pronograde leap	0.04	0.10	0.20
Drop	0.36		
Unimanual suspensory drop	0.57	0.70	0.90

Locomotor Mode, *submode*[a]	**Ketambe**[b]	**Suaq Balimbing**	**Sabangau**
Bimanual suspensory drop	0.04	0.10	0.20
Sway	4.55	14.90	19.00
Ride	0.50	0.60	0.80

[a] Locomotor descriptions follow exact definitions of Hunt et al. (1996) and Thorpe and Crompton (2006)
[b] Frequencies for Ketambe taken from Thorpe and Crompton (2006)

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A

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